



*The
International
Fancy Guppy
Association*



**IFGA EXTRACTS
BOOK ONE**

IFGA EXTRACTS

FOR IMPROVED GUPPY STRAINS THOUGH KNOWLEDGE

.....and a measure of LUCK!

This volume of IFGA Extracts is dedicated to the many investigators, past, present and future, who throughout the years slowly continue to unravel the complex secrets of life, reproduction, and heredity by which we can better adapt and influence some degree of control towards the goal of improved health, size, vigor, color and shape through a dedicated program of selective type breeding of quality stock.

FIRST PRINTING .EDITION JULY 1985

With illustrations

IFGA EXTRACTS - Volume I..July 1985 —p 1

FORWARD

This volume has been assembled to serve as a source of information for the new guppy breeder and as a reference of the findings and trials of other breeders. A wealth of information and hands-on experience exists concerning guppy breeding by the countless hobbyists who have enjoyed raising the guppy for years. Several books have been published about the guppy and contain the authors views based upon his tank conditions and strains. However, it is no secret that what works for one person does not work for another, especially where guppy breeding is concerned.

Water conditions differ throughout the country, strains differ by virtue of their purity, feeding habits effects growth and color and so on. Who is one to believe! Believe every one for what they have been able to accomplish but don't copy their methods and expect the same results. Instead read about as many different experts and their methods as possible. Then as you try different procedures, you have more of a wealth of background knowledge to formulate your own trial methods until you find what works best for you in your environment. Perhaps after a few years your strain improvement becomes stagnant and you can again review your records and compare results from other breeders. It is earnestly hoped that this volume is only a beginning and that as others write about their particular findings, both successes and failures, this volume will be updated and revised by either correcting some of the present articles, eliminating some and/or adding newer concepts and views. This volume is stored on 40 track TRS 80 disks to make the task of any future editing as effortless as possible. Only by writing and making permanent records and by publishing our results can we effectively contribute to the advancement of the guppy hobby.

If you feel you have views, experiences, or records concerning genetics or breeding and would like to share them in an article, please do not hesitate to contact our staff. We are ready to help you in any manner possible

TABLE OF CONTENTS

Hybridization "Look before Crossing"	Tom Hayes	9
Hybridization	Bob Fisher	9
How to Outcross Guppy Strains	Midge Hill	11
The Wonder Of Hybridization	Anonymous	16
Breeding Techniques	Jack Rosengarten	16
Inbreeding - Fact and Fiction	Jack Rosengarten	19
Outcrossing, Adding Recessives, Line Breeding	George McCroskey	20
New Developments in Fancy Guppies	George McCroskey	24
Line Breeding	Joseph L. Tuppler, Jr.	27
Inbreeding Guppies	Ronald Hood	29
Methods of Restricted Guppy Breeding	George McCroskey	31
Choosing Breeders	Bob Fisher	35
Guppies, Fact or Fantasy	Frank Daye	37
Variety in Guppies When Space is Limited	Midge Hill	38
Why You Cannot Raise A Good Show Guppy	Bob Maxwell	41
The Best is in There Somewhere	John Wolcott	43
Selecting Breeders	Elvis Bryant	44
Inbreeding, Fact and Fiction	Jack Rosengarten	45
Separate Quarters	Stan Shubel	46

TABLE OF CONTENTS GENETICS

GENETICS AND BREEDING - DR. JOSHUA H. WILSON

Introduction	49
Part I Monohybrid	51
Part II Dihybrid	55
Part III Genes And Chromosome Theory	60
Part IV Recombination and Mapping	71
Part V Inbreeding	77
Part VI Crossbreeding	86

MAKING GENETICS WORK FOR YOU - DR. EUGENE C. LARR

Part I Introduction	92
Part II Mutation	94
Part III Sex Chromosomes	96
Part IV Hormones	98
Part V Zebrinus Trait	100
Part VI Test Crosses	102
Part VII Breeding & Delta Tail Study	104
Part VIII Delta Tails, The Female	106
Part IX Breeding Program #1	108
Part X Breeding Program #2	109
Part XI Linebreeding	110
Part XII Outcrossing	112

THE TRUTH ABOUT GUPPIES - TONY ABEL

Outcrossing, Adding Recessives, Line Breeding	114.
---	------

TABLE OF CONTENTS

GUPPY GENETICS

Part I	Introductory Terms	117
Part II.	Monohybrid Cross	120
Part III	Sex-Linked Genes	123
Part IV	Dihybrid Cross	127
Part V	Slightly Mathematical	130

Guppy Genetics - Some Facts and Fallacies	Jack Kelly	132
Atomic Age Guppies - Creating New Varieties	Charles O. Masters	133
The Genetics of the Delta Tail Guppy	Albert J. Klee	135
Non Sex Linked Factors	Albert J. Klee	138
A Little bit about a Big Subject "Genetics"	Joe Sienzak	140
Breeding the Guppy	Bill Thompson	142
Guppy Points to Ponder - Outcross for Vigor	Arthur Lietze	144
So You want to raise good guppies.....	Henry Kaufman, Improving the Strain.....	145
New Studies on Dominant and Recessive Genes	Astrid Young	148
The Genetics and Breeding of Guppies	Albert J. Klee	149
Growth Pattern in Guppies	Henry Kaufman	152

HYBRID VIM AND VIGOR

Opinion Number One	William L. Brown	153
Opinion Number Two	Ray D. Owen	154

GUPPY BREEDING



HYBRIDIZATION

LOOK FOR... PERHAPS WE SHOULD SAY THINK! BEFORE CROSSING

by Tom Hayes

One goal of every serious aquarist is to "*come up with something new*." Certainly there is nothing more exciting than discovering that one (or several) young fish from a brood is different from its brothers and sisters in coloration or finage, and is perhaps the first of its kind. I'm sure many a hobbyist has had this experience and has envisioned himself as another Hahnel (originator of the fancy guppy) or Simpson! (Originator of the hi-fin swordtail). I'm also sure most hobbyists with this experience have been disappointed for those unique creatures usually turn out to be undersized, sterile, or if they grow to normal size and are fertile, fail to produce duplicates of themselves.

The kind of fish I've just described is a mutant, which occurs by chance not by design. Well, then, why not try to create a new fish by design? Why not hybridize? After all, won't this result in not one but many fish of a new color pattern or finage? The answer to this is "possibly" and only possibly. Furthermore, the result maybe disappointing: Before experimenting with hybridization to "see what happens" the following points should be kept in mind.

1. Crossing fish of different colors does not necessarily mean offspring sporting a combination of both colors. The genetic makeup of the fish determines the color, that is, if one color is dominant all the young maybe of that color (although future generations will produce some of other colors).

2. New hybrids often are sterile or of low fertility. A friend of mine developed a striking fish, but the strain has never been established as 90% of them have been sterile. This has been the fate of most hybrids despite the many beautiful strains of guppies, swordtails, platies, mollies that have been developed. And where established a hybrid strain has been successful, it was usually only after several generations of fish. So, even if a fancier is successful in establishing a new strain of fish, the entire process may take several years.

3. Not all hybrids are beauties. Is hybridization truly successful if the product is unattractive? A colorless or washed out fish certainly will not adorn your living room show tank. Neither will a local retailer be impressed with the uniqueness of an ugly fish that will not sell.

4. Experimenting with fish usually requires the use of a number of tanks as well as a number of fish. The beginning fancier, or the fancier with limited space, would do well to stick to the more mundane breeding combinations. Also, specimens for hybridization experiments should be as perfect as possible (if culls are going to be used...forget it.) The fancier with limited breeding stock cannot afford to use his prime fish for experimentation.

HYBRIDIZATION

by Bob Fisher

The dictionary defines the word "hybrid" as being "the offspring of two animals or plants, of different races, varieties, species etc. Anything of mixed origin". If we look at the modern fancy guppy with this definition in mind, we must conclude that almost all fancy guppies are hybrids, because there are few

"pure" strains around today. Such strains as do exist are to be greatly valued for their breeding potential in creating new hybrid varieties.

Every time a breeder puts a pair of guppies together for breeding, he is conducting an experiment in genetics and heredity. If the two fish are from two different strains he is creating a hybrid. His hope is that the good features of each parent "strain" will be combined in a single hybrid line. Sometimes he is lucky and the fish that emerges as the result of a random cross is much bigger and better than either of the parent lines, but all too often the result of a random cross is degeneration and reversion to wild features. The difference in the outcome of course, depends on the quality of the parent stock. Many beautiful fish are offered for sale and claims to be "strains" the buyer having no proof other than the assurance of the breeder selling the stock. They cross this new "strain" with their carefully produced stock only to be disappointed when the hybrids fail to measure up to their expectations. Instead of a tank full of guppies displaying every characteristic from "a" to "z".

Genetically, this mishap can be explained as follows. If a pure strain "AA" is crossed with another "pure" strain "BB" the resultant hybrid individuals will be "AB". Every single guppy in the mating will inherit a complete set of "A" chromosomes and a complete set of "B" chromosomes from one or the other of the parents. Thus it can be expected that in the first generation, all of the hybrids will be "AB" individuals and should look alike and possess similar characteristics. They should all possess the same color, even though the color may not necessarily match either of the parent strains. So here is one way to test the purity of a strain. If the first generation individuals look alike, it is pretty positive proof that the parents came from fixed strains. If the guppies in the first generation hybrid cross give about 50% of one type and 50% of another type, it can be deduced that only one of the parents was from a fixed strain and the other was itself a "hybrid". To illustrate, let us consider mating an "AA" individual to a "BC" hybrid. The result of this mating will produce 50% "AB" hybrids and 50% "AC" hybrids.

Now, if we follow the same line of reasoning and deliberately cross two hybrids, it is possible to get that tankful of junk where almost every individual is a "mongrel". To illustrate, suppose we mate an "AB" individual to a "CD" individual. The following possible combinations of chromosome packages can occur, "AC", "AD", "BC" and "BD", roughly 25% of each. Now each of these new combinations could be a superb new hybrid, but adversely, the reshuffling of genes could bring about the reversion to the old stock so I often witnessed. The chances of success or failure run about 50/50again, success depends on, the quality or "purity", of the parent strains "A", "B", "C", "D".

Now this is all theoretical and does not take into account the fact that approximately 10% of all guppies are mutants, meaning that genetically their composition has changed very slightly either by a crossover in the chromosomes, or the addition of some genetic material (a mutated gene) or the loss of some genetic material (a changed or destroyed gene). If we consider these factors playing an important role, as indeed they certainly do; it is conceivable that in addition to producing 4 basic varieties from crossing two hybrids; we will also have included a small percentage of mutants to further confuse the picture.

Unfortunately no guppy breeder has a crystal ball and is able to fully predict the outcome of a particular mating unless he is "line breeding" fixed strains where it is much more possible to call the shots. This then points out the importance and value of the fixed strain. If any line of guppies will consistently deliver 90% or better. Individuals all possessing the strain features, then one can assume he has a fixed strain and can also assume that this strain will continue to produce its like in successive generations providing the small percentage of mutants are not allowed to break the genetic inheritance.

Deliberate hybridization of fixed strains is a very worthwhile practice. Many prominent guppy breeders produce their best show stock this way, mainly because hybrids have renewed vigor and generally grow considerably larger than the fixed strains which produce them. I call to mind an experience of about 15 months ago, I obtained a fixed strain "yellow" female from a prominent breeder, having no male to go with the female I was forced to breed her to one of my own lavender multi-color males from F1 strain which was only four generations old. The hybrids this pair produced were the best I have yet produced for size, color and show quality. The color of the hybrid males was a red, white and black multi-color with the red predominating. The finage, however, was far superior to either of the parent varieties and thus these fish for a short period, claimed several prizes in the show circuit. I then tried to line breed these fish and could not duplicate the effort, their offspring were a miserable concoction of everything from "a" to "z".

However, going back to the original strains and producing the first generation hybrids, I again did the trick. Thus, in order to produce these outstanding hybrids, I am forced to keep two additional parent strains in order to provide breeders for the hybrid line. This is not a new experience, many breeders do the same thing. I record it mainly to illustrate the fact that "hybrids" have to be produced randomly, but with some effort and forethought. Hybridization can be very worthwhile, but caution should be exercised by the novice. I believe that before one undertakes to produce a hybrid, it is essential to know the genetic construction of the breeders.

It is seldom one visits the home of a first rate breeder without seeing these types of breeding experiments taking place. I usually have at least half a dozen crosses going in order to assure future show stock. However, for every ten of the crosses I try, only one will be successful and give me what I was after.

The fact that hybrids are only good for one generation causes problems in that so many parent strains must be maintained in order to assure future breeding stock for the successful hybrid lines. The most practical way of achieving a consistent supply of hybrids is to carry only one or two parent strains. If one then retains a few virgin females from these strains, he has a ready supply to mate with any promising male he can procure from other breeders.

I find it fascinating to watch how different gene combinations can produce different effects in the hybrid offspring. But, while hybridization is interesting and important for the future of the guppy, it is the maintenance of the "pure" strains which will assure genetically correct material for hybridization.

(Reprint from "The Guppy News". Int'l Guppy Breeders Assoc.)

HOW TO OUTCROSS GUPPY STRAINS

based on a program given by Midge Hill to S.C.G.A.

We all know that the best advice one can receive (and follow) on how to breed show guppies is "...get a good-quality, well-established strain and then keep it as pure as you can by inbreeding or line breeding.

Outcrossing is the opposite of inbreeding because it involves mating of fish that are genetically unrelated. The reason that most successful guppy breeders outcross strains from time to time but seldom advise others to try it, is because outcrossing is really a form of genetic Russian roulette. A successful outcross requires that the strains crossed be genetically compatible. The odds against finding two compatible strains are very high.

There are times however, when outcrossing may produce something that no amount of inbreeding within a strain will accomplish. There are times when your only alternative is to outcross for example, when you buy a fish at a show auction without a mate. Fortunately, there are ways to improve your chances of getting good result from an outcross, how to pick the outcross strain, and how to proceed after

the initial outcross to get the best subsequent generations.

Before getting into the good reasons for outcrossing, I want to mention that there are a lot of no-good reasons for outcrossing. Now there is nothing wrong with outcrossing just for the sake of idle curiosity, but it is wrong to pass these fish along as good breeding stock. What outcrossing does is to scramble together the genetic patterns of the two parents, therefore, offspring from an outcross are genetically all mixed up.

Getting back to the good reasons for outcrossing, there are five situations in which outcrossing can be a good thing to do:

1. When an established strain will not produce a characteristic you want (a larger dorsal, perhaps) because the gene pattern for that characteristic is not present in the strain.
2. When you are having trouble with an established strain, such as infertility, maybe.
3. To produce big show hybrids.
4. Necessity, as in the case of a male purchased at a show auction with no female.
5. To create your own strain.

Lets discuss each of these five situations in detail to explain why outcrossing, as chancy as it is, can be a good thing to do, and how to proceed after the initial outcross, because the breeding techniques are a little different for each type of outcross.

In the first situation, where you have a good established strain but you have been unable to get a certain feature you want by inbreeding or line breeding within the strain, outcrossing can be the solution. Lets say you have been working with a strain of reds which are not as bright a red as you would like. Dr. Larr has found that there are at least four different genes for red color. If your strain does not have all of these genes, no amount of inbreeding is going to produce what is not there to begin with. So, you will have to outcross to add the missing genes that are needed for a clearer, brighter red. Or, perhaps you have been trying to get a larger dorsal. You, might be able through inbreeding, by careful selection of parents, to gradually over the years get a larger dorsal maybe. But there is a chance to use an outcross to pick up a larger dorsal in less time.

It goes without saying that you do not want to lose the fine characteristics of your original strain. So, while you are trying an outcross, 1 you must keep your established strain going: not only to guard against loss of the strain if the outcross does not come out well, but also because you will need to have breeder from the pure strain to work with in order to incorporate the hybrids with the desirable added feature back into the pure strain.

What strain should be selected to outcross into an established strain when attempting to add a new feature to the established strain? First, the outcross strain should also be a well established one that has bred true over many generations so that all the males in each litter look very much like previous generations. The outcross strain should be the same type as the strain you are going to outcross it to. In other words, outcross red to red, blue to blue, half-black red to half-black red etc. And obviously the outcross strain must have the particular characteristic you are looking for.

When you find a strain that meets the above requirements as closely as possible, you make the outcross both ways. Take your best male, and mate him to females of the "outcross" strain and also take a male from the outcross strain and mate him to females from your original strain. You do this because you do not know which way will come out the best and there is often a marked difference in results. And, of course you keep the young separate so you can determine which was it that has been most successful.

If you find a male in the first generation (the F1) that looks like your original strain and also has the new feature from the outcross strain that you were trying for. Well you are just about as lucky as it is possible to be. What has happened is that: the feature you wanted to pick up has proved to be dominant, and so it appeared in the first generation. When this happens, you breed this F-1 male back to females from your strain, you want to work back into your original strain as soon as possible after making this type of outcross. Since the trait has proved to be dominant there should be fish in each succeeding generation that show the trait. The breeding program is continued by breeding the best male with the new added feature back into females of the pure strain that you have kept going on the side. We have been talking about an outcross that produced the desired features in the first generation. Most outcrosses will not be so lucky as to show the desired feature in the F-1....but that does not mean it is not there. There are two reasons why a feature possessed by a strain used in an outcross may not show up in the F1; a) the feature is recessive, or b) it is carried only by the females.

If the feature you want does not show up in the F-1, you should breed brother and sister from the F-1 litter together. If the trait is recessive, it should show up in 25% of the offspring from this sibling breeding. Assuming that the trait turned out to be a simple recessive and showed up in 25% of the F-2, you select an F-2 male that looks the most like your original strain which you have kept virgin exactly for this purpose. The recessive trait will again go into hiding in the offspring from this mating, but all the young will carry the trait and by breeding a recessive trait back into an established strain which does not carry the trait, you have to use a two-generation cycle, every other generation you will breed siblings and in the alternate generations you will breed back to the pure strain females.

You remember we said there might be another reason why a trait would not show up in the F-1....it might be that the new trait was passed to the F-1 females, but not to the F-1 males. Therefore, besides breeding brother to sister from the F-1 to see if the missing trait is recessive, you should also breed some of the F-1 females to males of your original strain on the off chance that the trait had been handed down by the outcross males on his X-chromosome ... which goes only to his daughters. If this is the case it will show up again when these daughters are mated to either their brothers or back to the original strain males...but in the latter case you are a generation ahead in incorporating this desired feature into your original strain. From then on each future generation is bred by mating pure strain males with females from the hybrid line which with each successive generation will get closer genetically, to your original strain.

In summary, when an outcross is used to try to add a feature to an established strain, one of three things will happen in the first generation:

- 1) the desired trait is dominant,
- 2) it will not show up in the F-1 because it is recessive, or
- 3) it will not show in the first generation because it is carried by the females.

The dominant trait and the trait carried by the females are the easiest to handle. The recessive trait is more difficult. But in all three the whole purpose is to breed the new trait into your original strain as often and as soon as possible.

Now lets go to the second outcross situation. This is the case of an established, highly-inbred strain which has developed a major genetic flaw such as infertility, a high percentage of crooked spines, susceptibility to disease, etc. An established strain which is rapidly going downhill because of a genetic problem, but which is still beautiful in other ways) can sometimes be rescued by careful selection of breeders without resorting to an outcross. You would certainly want to try this first.

Let me say here that inbreeding guppies, even very close inbreeding, is not of itself harmful. Guppies will take close inbreeding for many generations without significant loss of size or color or vigor. When highly inbred strains develop serious genetic defects, and they often do, it is not because they have been inbred for too long a time, but rather because the breeder picked the wrong fish to use as parents.

But, what if your established strain just gets worse, no matter how carefully you try to pick the best parents, you can try an outcross. You should still try to keep the original strain going if you can, because you should bring back the outcross hybrids into the original strain as fast as you can.

You would use the same criteria in selecting the outcross strain as were used in the preceding outcross situation. Again, outcross both ways if at all possible, and again, keep the offspring from these matings separated until it can be determined which mating was most successful. When these F-1 hybrids are old enough to select breeders, breed the best male from the F-1 back into your original strain. It might also be wise to also breed one of the hybrid females to the best male available from the original strain just to see which method of breeding gives the best results. If the weaknesses start to show up again, back up and breed the hybrids sibling to sibling until the fault disappears again.

Perhaps I haven't said enough about why you want to outcross the strain to be a well-established true-breeding strain. Remember, that what an outcross does is to scramble together the genetic patterns of the two strains which are crossed. If one side of the cross is itself only a few generations away from a previous outcross, all you have accomplished is to further mix up the genetic patterns. Long experience and experimentation have proved that these hybrid-hybrids may look good for a few generations, but that their mixed up gene patterns soon cause them to regress back toward a small, motley fish.

Now, to the third situation in which an outcross can be desirable to produce big show hybrids. If you are very lucky and are willing to devote tank space to an endeavor with very long odds, you can keep trying outcrosses of two unrelated established strains hoping to find a cross that will produce outstanding results in the first generation. If you do stumble onto one of these compatible combinations that throw big beautiful - show specimens in the F-1, guard the two parent strains carefully.

One unique thing about this type of outcross is that there is no breeding program after the outcross. In fact, you do not breed from hybrids at all, but rather keep and inbreed both parent traits separately and outcross the two traits continually to each other to get your show specimens. Another advantage is that since you will not be breeding from these hybrids, you can discard the females as soon as they are sexable...no need in wasting food, time or space on them. The hybrid males are raised for show but are never bred either. Many breeders have used this method to produce their top show fish.

Another unique thing about this type of outcross is that often the strains that turn out these fantastic hybrids appear to the eye to be very inferior fish, but they are usually also very inbred. For example, one highly successful outcross that works well for me involves using one strain of small veil tailed guppies that carry brilliant color to cross to a strain of big-bodied, big-tailed blah-colored fish. The F-1 hybrids of this unlikely combination are large, beautiful, bright-colored fish which have won their share of international trophies. But, breed these F-1 hybrids together and all you get is junk.

Outcrossing by necessity is the next situation. Purchasing males without related females is the most common instance in which outcrossing becomes a matter of necessity. Having purchased a fish, you will need to decide what direction you want to go with him before choosing the female to outcross him with. You should decide what you like about him...why did you buy him in the first place? Was it his flowing dorsal, his color or what? Once you decide this you should look for a strain to outcross him to that is already well-established and which you think will best preserve the feature you bought him for. Almost

without exception, the outcross strain should be similar in color, or at least the same basic caudal color.

For example, lets say you bought a green snakeskin male at a show auction: . The best outcross strain to keep the green color would be a good green strain but it doesn't have to be snakeskin since the snakeskin pattern will almost always be carried by the male so will usually appear on all of the male young produced by the snakeskin, no matter what kind of female is used.

If the male you purchased was a gray bodies type, you would probably select a gray-bodied strain with his same basic caudal color to outcross him to. If he is an albino a gold or a bronze he can be outcrossed to a gray-bodied strain. Although all of the F-1 will come out gray-bodied they will all carry the other body color which will show up in 25% of the fry resulting from a cross of two siblings from the F-1.

When you have selected your outcross strain, you should acquire enough breeders from that strain so you can keep the strain going pure in addition to making the outcross with the male. Because the best way to establish a strain from this lone male is to continue to breed the hybrids back into the already established strain. This is the quickest way to get the hybrid strain. With each generation the hybrids will get more and more like the established strain you are working them through. If you begin to lose what you liked about the hybrids in the first place start breeding the hybrids brother to sister.

The reason I do not recommend breeding back to the original auction male is that nine times out of ten you will know nothing about the fish. You do not know if he was from an established strain or if he is the result of a wild series of outcrosses. The chances are pretty good that he is a hybrid or not many generations away from an outcross. You have outcrossed him again, which makes his offspring hybrid-hybrids. Breeding him to his daughters, in this instance, will just mix up the gene patterns even more. If you have the tank space, go ahead and try breeding his daughters back to him. You might get some show males, but to set a strain it probably wont work.

If that male you purchased was from an established strain, that is a completely different thing. In this case, both sides of your outcross were established strains. This is when you may successfully set a new strain by breeding him to his daughters, to his grand daughters, etc., if he lives long enough.

The fifth situation in which you must know how to set a strain after an outcross, is if you have the desire to create your own special strain. The idea of continuing, even very successfully, somebody else's strain just does not appeal to some people. If you are one of these, you can create your own strain. You would probably start by outcrossing a fish to a completely unrelated strain hoping to preserve the best qualities of each strain. Or a color mutation of some sort may appear in your own tanks and you might try to build a whole new strain from this mutated type. No matter how you start out, the idea is to purify the new strain as quickly as possible, and all of the principles already discussed apply equally here.

If you started with an outcross, breed the hybrid males to females from the established strain used in the outcross. If you were lucky enough to have well-established strains for both sides of the out cross, you can also mate the hybrid males to females from both of the strains used to see which gives the better result. If you started with a mutation through the pure strain females to set the mutated feature.

I think the half-black pastels have had more outcrossing done to them since they first arrived from Germany than any other type at the moment. Outcrossing of the H/B pastels was usually necessary because the Germans do not send females. This outcrossing has produced some beautiful fish, but a lot of half-black pastel strains are deteriorating too. Not all of these outcrossed strains have continued to produce good fish generation after generation. You can not keep on outcrossing every few generation without

finally scrambling up the genetic patterns to the extent that the fish just deteriorate into a nondescript nothing

In summary, first, outcrossing is not the name of the game at least not for very long. The real challenge of this hobby is to be able to set and then maintain a true-breeding strain which will produce beautiful fish generation after generation, show after show. And second, if you outcross, for whatever reason, don't palm off these mixed up fish as being good breeding stock.

(Condensed from "Guppy Gazette", Aug. Through Oct. 1973)

THE WONDER OF HYBRIDIZATION

Anonymous

While hybridization has definite advantages, it also has disadvantages. In order to get one, you must resign yourself to the other. To my knowledge, there has been no quicker way invented to improve the appearance of guppies. Two poor appearing fish can be crossed together and - the resulting young will be so unlike the original parents as to be unrecognizable. (Often the hybrids are better looking than either of the parent strains).

The method of outcrossing guppies sounds like the perfect method of getting good fish, which it is, provided you have two lines that will make superior guppies when crossed. The majority of crosses of two unrelated lines of fish will not be successful, meaning the fish will be poorer in physical appearance and possibly lacking in a wanted trait of the original parents. Another disadvantage is that the hybrids will not breed true in the second generation offspring. Often the young begin to separate out into mixed up versions of the original strains in certain percentages, which makes them useless for all practical purposes of breeding, because the genetic makeup becomes so mixed up.

Opposite to the hybrid guppy is the inbred kind, which have been bred together for some generations to concentrate certain characteristics. This also concentrates the unwanted traits so that after some period of time the highly inbred guppies may appear so poor as to be unwanted by people who do not know the fish for what they are, BUT...the better the breeding stock is inbred, the better the resulting hybrid crosses are likely to be. The better hybrids are often made from very poor appearing strains that are specially bred for the purpose of creating hybrids.

(Super condensed for "F.T.F.I. Trader", August 1967)

BREEDING TECHNIQUES

by Jack Rosengarten

Lets take a look now at some of the techniques of breeding guppies. I hope that most of you are convinced that the best method, although sometimes impractical for a particular breeder is to isolate one male with one virgin female and to isolate their offspring until they mature. This offers an opportunity to be sure of the parentage, what they looked like, and of course, what the results were.

Quite often breeders will use a method known as population breeding. This involves putting several of the best males and females together and allowing all the fry to mix. The next set of breeders is selected from the fry population. The advantage of this method is that precious time is not lost if one of the fish is sterile, dies, or turns out to be the wrong choice. I'm sure that many breeders also feel that they will also

get many more combinations than if they are paired off in separate tanks. The disadvantages of this method, however, are legion.

It has been pointed out that quite often the odds against selecting the best female when breeding for male traits, are usually pretty large. If the probability of selecting the best female is one in four, then the chances of selecting the two best females is only one in sixteen, and of selecting the three best is only one out of 64 times, in other words you may be lucky enough to choose the best female if you choose only one, but trying to select several and mixing their fry will be almost sure to dilute the results. Likewise if several males are used the chances are that only one of them will do the mating, and unless they are perfectly matched, you can be sure it is the smaller one with the smaller fins. This is not some perverse Murphy's Law (if there is a wrong way it will happen), but an example of, Darwin's survival of the fittest. Whenever guppies must compete, whether it is for a mate or for food, the ultimate result will be reversion to the wild type. Since I work with a small number of tanks, I have been forced to compromise between the two methods and have evolved a number of rules which are presented below:

1. Start with your best male and several females. If the female candidates do not look like each other be sure to select one of each type unless you have already decided on a female type. If the females are not heavy in three weeks, add another male.
2. Remove each pregnant female to a separate tank to deliver her fry. As available tanks permit, keep each set of fry separate. Make sure you have classified the mother and can still identify her if she is to be mixed with other females. This will be important if she is to be used for backcrosses. Some breeders snip off a piece of the caudal to mark her.
3. Continuously use new brood females obtaining them from the matured fry. Using the same female over and over will never improve the strain. I usually keep only one or two litters from a female and then retire her. The females are not put back with the males.
4. If space is not available for keeping several litters separate, keep at least the most promising one separate.
5. As the separated litters mature, compare them to the mixed population. If they are worse, dump them; don't mix them back into the population. If they are better, dump the population and make the best litter the source of your new breeders.
6. Separate the male and female fry as soon as possible. This will assure that the females remain virgin. Since the females can carry the sperms for months after a mating, a mated female can ruin a breeding program in some strains the first indications of sex are when the males start to show color. In other strains the first indications are when the females start outgrowing the males.
7. The new stud males can be chosen from any of the litters. The brood females should be selected from the litters that have the highest percentage of desirable males even though the best males are not in the same litter. Of course, you may want to backcross to the original sire if he is still the best male.
8. Above all be sure that immature males are not allowed to mate. They are an unknown quantity until fully mature. Occasionally you may breed a promising young male, but have the courage to admit when a mistake is made.

9. Cull early, but wisely. Sometimes the ones that mature the slowest are the best. Learn the characteristic color changes as the fish mature so that you will know at the earliest if the desired results are forthcoming. Make note of how many you cull and why since this is an important statistic. If you are trying for a particularly hard combination, it might be prudent not to cull until all have matured. Perhaps what you are trying for is liked with small size or some other trait you consider undesirable. It also may be a rarity and you may miss your only chance.

10. Never breed a deformed fish. Although my experience has been that most deformities can be traced to environmental factors, enough are hereditary to bar taking chances.

Remember, the above rules are a large improvement over population breeding, but are no substitute for the breeding of selected pairs and the separation of all litters. If you are trying to improve more than one strain with a limited number of tanks, it may be wise to dedicate most of your tanks to one strain at a time while only maintaining the other strains.

Now some words on selecting the females, assuming that your goal is to raise male show guppies. Most cases, the females will not display the traits that you are trying to establish in the males. Body colors and half black patterns are the notable exceptions to this rule. The usual advice when breeding for detail is to select short, thick females with large dorsal fins and wide caudals.

The major trap that many breeders fall into is that of double selection. Simply stated, this is attempting to select both the males and females for their good looks. All the genes of a guppy are located on one of 23 pairs of chromosomes. Selecting a female characteristic may assure that you exclude a desired male characteristic.

My own experiences bear out the pitfalls of double selection. When I started purifying my doublesword snakeskin line from a strain which also produced vertical snakeskins, I selected females with caudal patterns that suggested doublesword snakeskins. As the line deteriorated, I finally realized that my best results were coming from matings with females that had clear caudals and that is what I now use. Right now I am trying to establish a red delta line and although many of the females show red in the caudals, am slowly forming the opinion that my best results came from females with black caudals. It is conceivable, but entirely speculative, that a female may be able to display one gene because another gene on the paired chromosome modifies it, but may be unable to express a pair of the same genes because the modifier is now excluded.

What must be done is to classify your female fry as well as your male fry. Look for basic differences. They may include fin shapes, body proportions or color markings. When you select your first set of breeders make sure that you choose at least one female from each type. Check the next generation of females in each litter. Do the female fry look more like their mother and the males less like their father? If so, it may be a coincidence, but it may also be significant. Do the litters from the different types of females show the same scattering of female traits or is some trait starting to become more prevalent? Is a litter high in one female trait and low in some male trait while the opposite is true in another litter?

Even if the female fry are starting to look alike, it may not mean that the females appearance is contributing to your goal. It may mean that you have found a safe set of chromosomes that will at least not detract from your goal.

Although all of the preceding has favored the breeding of show males, they are equally applicable to the breeding of show females. In fact, the danger of making an unwise double selection is more prevalent since the males display considerably more than the females. Good show females have long slender bodies

while, as previously mentioned, short thick females are recommended for breeding to males. So perhaps the small finned males would be best if you are after show females. I recall at least one breeder writing that he discovered he was culling his best breeding males. The half black strains are a notable exception to the above as some produce show winning males and females in the same strain. Which breeders to choose is something that you must determine by trial and error. I hope that this article provides you with some of the necessary tools.

INBREEDING FACT AND FICTION

by Jack Rosengarten

Many things have been said about the evils of inbreeding, but little seems to have been said about the true facts. Inbreeding can be either good or bad or both, depending on the talents of the breeder and a certain element of luck.

Simply defined, inbreeding is the mating of closely related individuals. This has the effect of allowing recessive characteristics, which normally would stay hidden, to be displayed. Closely related individuals can be expected to be carrying the same recessive genes, and therefore some offspring will receive a pair of the genes, which is what it takes to display a recessive characteristic.

Inbreeding, or incest as it is called when applied to humans, is frowned upon by society, because of the well-documented occurrences of hereditary diseases in such relationships. Horse, cattle, dog and cat breeders avoid inbreeding for the same reason. Fish breeders think the same way, but should they?

Inbreeding concentrates all of the recessive genes, the good and the bad. What then is different about the inbreeding of the higher animals and fish? In a word, NUMBERS! Horses and cattle usually have one baby at a time. If an undesirable result occurs, it is costly and time consuming. Dog breeders also have small litters, so that inbreeding is chancy. Fish, however, have large litters which yield a closer approximation of the hereditary ratios developed by Mendel. Inbreeding does not create deformities, it merely makes it more possible for them to be displayed. Likewise, those longer fins, purer colors and greater size can also come to the forefront instead of staying stay-in-the-background. With large litters the breeder is not faced with a total loss if something goes wrong. In fact, he can expect something to go wrong and he can also expect something to go right. That is where culling is important. A good breeder will select the best pair to be bred very carefully. If he is lucky enough to have a lot of tanks, he should select a number of pairs so that as long as one will not be lost if one wrong choice is made.

Many breeders will use schemes to provide insurance against running into a dead end. Either by using a crisscrossing method or inbreeding separate lines of the same strain. Some will combine both methods by crossing the lines after some number of generations. For breeding show male guppies, I prefer line breeding with as many pairings as possible since the females can truly only be selected by trial and error or at best an educated guess.

Records are important so that the breeder will know when something is going wrong. Ignoring the first indications of something going wrong, indiscriminate inbreeding, or population breeding where the true parents cannot be determined are the common pitfalls of a poor breeding program. Numerical counts of the good and bad results will let you know if the goals are being achieved. Merely culling every time a defect is spotted without recording the fact, is living in a fool's paradise. This is the reason many breeders show spectacular results for a year or two and then lose the strain.

What should you do if a strain is deteriorating? Most breeders will dump them and buy some new stock (from someone who knows what they are doing, and start all over again. 'What a waste.' Breed your strain to a closely related strain, and with a carefully determined program, breed out the undesirable traits and whatever effect the outcross cause. This will be much easier than starting all over.

In summary, inbreeding requires precisely administered techniques in order to be of value. You also will discover that inbreeding will turn up many new characteristics because the mutations and crossovers which frequently occur will now start to show up instead of being lost without ever having appeared.

Reprinted from Guppy Roundtable, Feb. 1975)

OUTCROSSING, ADDING RECESSIVES, LINE BREEDING

by George McCusker

Any guppy nut with poorer guppies than he would prefer will always come up with the comment on the drop of a hat "This stock needs new-blood" or in other words, a couple of new fish to add into his own would likely cure things very nicely. On which comment, a lot of misrepresentation can, and often does happen.

For the sake of the subject at hand, let's say you just happen to be one of the people as stated in paragraph one and you wish to obtain some "new" quality guppies for the purpose of breeding with your own. If you follow the general trend, all you actually wish is some new guppies that 1) LOOK better than your own and are of approximately the same color, and 2) these are within your means financially and otherwise. I think that past experience will show that the average guppy hobbyist assumes that once he can fulfill the above two needs, from then on he will have a "made" To which statements I can safely say that this assumption is one heck of a poor way to proceed, except for the occasional individual who has more luck than is good for him.

Like most everything that gives full returns for the money, and new blood that is added to existing guppies now on hand, a little advance planning and thought will be well-worth the time and trouble taken. The old time way of breeding guppies "by guess and by golly" maybe still used by those that have no better information to go on, but the modern methods of guppy breeding still makes the best sense and gives the best rewards.

It is only natural to want a new guppy male that is highly colored with a wide triangular-shaped tail and think this is the exact kind to add into your own fish. However, without some sort of background information on the parentage of the fish, it will be some months before you can know for sure what you actually have. At best if the guppy is totally unknown to you, the chances are 50-50 that you will even be able to get young by use of your own females from such a mating. Chances are even more slim that any resulting young will be an improvement to what you would normally have. It all narrows down to the fact that the truth about guppies is that seldom do they breed as you wish, or can reliably forecast. With unknown stock, and with doubtful genetic background, observing the offspring when and if these appear perhaps few personal examples, all true, will better put across what I am trying to say.

I was sent some excellent appearing blue deltas one time. The breeder who furnished these was the best known for these blues and it took some persuasion to get some of them. On arrival, they did look good, but somehow I had the feeling the fish were not as they appeared. So I did not attempt to blend them into my own blue stock. I am really not storing on blue guppies anyway. It took two generations of the strain to show up the discrepancy. They were heavily mixed with pale red guppies later on. I heard the

man overcrossed with reds at intervals to maintain the proper shade of blue. A person buying these fish, and using them to add new blood to his own pure blues, would likely end up with the most mixed up conglomeration of colors to where he would be worse off than he was when he started.

Just recently, two members exchanged guppies of a particular color. The less experienced of the two noted that the second generation of the fish he had gotten were all appearing with ragged tails. He immediately thought of disease, such as tail rot, or vitamin deficiency, or something similar. However, he did inquire to the other person in the trade who admitted the fish were originally from a strain of swordtail guppies not too far removed. This then was the apparent tendency of the young to revert towards the more dominant swordtail trait. A not uncommon occurrence BUT one that can be misleading if not known about. Let me take this trend one step further.

Some years back, when triangular tails were first appearing in small percentages of the more common velvet-tailed guppies, someone noted that the strains that showed up with the best triangle tails always seemed to show a very few male fish with some type of swordtail. Of course, like so many new things are, this was "laughed off" jokes about, and discounted as pure coincidence. Only a very few breeders kept quiet, watched closely and did some experimenting and observation to see if swordtail genes could be used to make better delta guppies. If any real progress has been made in this direction, scientifically speaking, I have not heard of it. BUT any guppy breeder of note agrees that any strain of guppies that shows up with an occasional swordtail male, is usually the best available. On the other hand, if one deliberately adds in more swordtail mating, the tail quality will show it very quickly as mentioned in the former example. Apparently, it is one of the narrow paths a guppy breeder must tread to do best, just allow a small trace of swordtail trait to mix in, but not enough to become so dominant as to effect tail strength and quality. My own private opinion, for whatever this is worth, is that the original strains of guppy formerly used to make wide tailed guppies, always were the very one to naturally tend towards sword. If anyone reading this can go away back when fancy gumpies were quite poor (comparatively) and we had mixed with common guppy types, always some male fish appeared with the typical swordtail. The same thing could be said for wild guppies back then, if enough fish were there to pick from, swordtail types could be distinguished. Even closer to home, if you carefully observe a top, bottom, or doublesword male guppy, and they are reasonably good, they have a good angle on the typical sword in the caudal. If you can imagine this open space between the points as filled in, invariably it would "make" a wide-tailed (even near-delta shaped) fish.

About three years ago, I read the theory that the addition of golds (or even albinos) to any fancy guppy strain would help to eliminate color mixtures and discrepancies. However, it was quickly shown that the use of albinos was hard to do as they were scarce, extremely hard to breed, not of the tail quality of most grey guppy kinds, and the addition of albino genes tended to weaken the strain in a number of directions. In comparison, gold guppies had flaws, too, but in a very different direction. Not many people cared to breed gold guppies. While small-tailed, gold guppies were fairly easy to procure, wide-tailed kinds were quite hard to come by, were usually mixed parentage and combining them with your best reds for the purpose of eliminating black coloring was only temporary at best, with the side-effect of decreasing tail width, inferior or less than true-bred gold stock. As so, people tried the opposite approach and attempted to add exotic colors to the gold bodied guppies with less than spectacular success for quite awhile. However, if enough people persevere, and enough exchanges of guppies take place eventually success of one sort or the other has to take place.

The best example pulled from my own experience, is the original half black guppies with a black tail.

These almost invariably were somewhere along the quite small percentages. Usually one was lucky to see two right colored fish (male or female) in a hundred baby half blacks. Which proved they were an extremely recessive type either due to being far back in the ancestry as compared to the half blacks on hand, or that the half black colored effectively suppressed the lighter color. Speaking for myself, it seemed to be a little of both and it took a lot of patience and time (plus tanks) to get either strain, half blacks or golds) to inbreed enough to where usable amounts would appear. Which brings up another point.

The coloring of gold guppies is recessive to the more normal, grey body coloring of guppies. This simply means that the gold color will not appear in the resulting young guppies from such a cross. But, if one takes a male and female from these same mixed breed fish, mate them together, then you will get gold colored guppies. The amount of these has been well worked out by laws of heredity and follows closely to these laws. If one takes the time to save, count and classify the baby guppies, 25% golds, 75% grey guppies, F-2. Any reliable book on guppy breeding, or genetic volume will give you this information so I will not bother to repeat the facts. To be brief, the percentages of golden young obtained by breeding brother guppies to sister guppies will gradually increase with the amount of inbreeding. If you have the desire to make a strain of true-breeding gold guppies.

By this time I can hear the readers complaints; "What will I gain by outcrossing to gold guppies?" Soaking it a logical step at a time, here is what one can reasonably expect to get, provided such is wanted.

Hybridizing, in its fullest meaning, is the act of cross breeding two unrelated species to produce "hybrids". The mating of a female horse to a male donkey, with the end product being a mule-hybrid is one such example. Regrettably, no real or accurate hybridizing of guppies has ever been done to my knowledge with this meaning a cross to some other type of fish. However, the generalized use of making hybrids is commonly used with fancy guppies in meaning to cross two strains of guppies that are not related to one another but are still guppies. To get maximum effects from such a cross in terms of vigor, increased body size, variation in coloring, or to "cure" partial sterility, it is best to use two guppy types that are as far removed from one another as possible, yet will make a compatible mating. In using the term compatible it simply means that the end results of the mating will give the wanted results. Such hybrid crosses are often ones that give inferior results or incompatible ones. By use of golden guppies, the two kinds of guppies are removed from one another genetically speaking, as far as possible with only albino guppies being further removed. Therefore, a cross of a normal grey guppy strain to a normal gold strain, will at the very least, potentially give maximum hybrid progress. This effect will be most immediately evident in the baby fish as they will appear larger and usually more active.

The mixing of gold and grey guppies has more far-reaching effects than the more immediate ones as stated above. However, it is only fair to mention that it does take some time, as measured in generations of guppies from the mixture, to see the more effective results. I am sorry to say that I cannot give reasons to why these effects happen, or even give plausible theories I have just noted they do.

INTENSIFYING OF COLOR: Breeders who carry guppies in somewhat acid water, or water that may lack certain minerals, but yet be fairly hard, will often complain about guppy coloration going "off" into other shades. Red, for example, going into pink or orange shades; Half blacks or 3/4 blacks with red areas often become a lighter blue rather than the wanted dusky black or a charcoal grey. Green fish may fade out to a whitish blue, blue guppies into a mixture of pale blue with either clear areas in the color, or into yellow. Other colors not specifically mentioned may become blotched, of a dull, rather than intense coloration. Regardless of the changes, they are not those wanted. While mixing in a bit of gold may not

be a cure-all for these ailments, it certainly will help if enough generations of fish are carefully kept and cultivated. Generally speaking, only one grey-gold cross will be needed for the effects to accumulate. It would seem that while the golden genes are recessive to most of those normally associated with grey guppies, eventually with controlled inbreeding they become semidominant and therefore, the full effects to show does take time.

VIGOR: Most any fancy guppy breeder knows that with continued breeding of any color of fancy guppy, the fish is apt to become smaller, less active, possibly semi-sterile, and often, with a loss in body size. An outcross to a related strain is the answer most often given to cure these ills, but if this outcross is to a kind of related golds, the effects will be more spectacular longer lasting, and less apt to inadvertently effect the coloration. One personal example that I have been carefully watching is a red strain that I got in a trade. At the time of trading, I knew almost nothing about it, had no idea the line carried gold guppies and knew only vaguely of the strain's origin. Twelve generations later, with close inbreeding, a good percentage of golds appear regularly, but even more important, the red coloration is excellent, tail width and shape is even better than expected and it is one of the most active strains of guppies I have.

COLOR CLARITY: To most guppy people who are active show participants, purity of color comes very close to the top in wanted characteristics. In the past two years, most breeder entrants have been specializing in improving color and this has brought up some odd theories. From my own personal observations, all colors of guppies I keep on hand have been seen to hold color better, hold it longer, and be purer in the one single color in the caudal and dorsal if they have some gold genes in the line. Assuming that my own experiences are not unique, I would suppose this same factor would help others.

BREEDING TIPS: As suggested before, one good reason for most guppy people not asking more advantage of outcrossing, is the lack of good, and reliable breeding type guppies to use. In the case of golden guppies, these are even more scarce. Guppies from commercial sources are often disappointing, those bought at show auctions are seldom good for breeding purposes, and I regret to say, guppy people needing new stock for making show-fish, are extremely suspicious of strangers. Therefore, with the quality of strange guppies one is likely to obtain, outcrosses are seldom what they could be. This is still no reason why they cannot be made to work — all it takes is more patience. Rather than seeing success in the first young from such a cross, it may be far better in the long run to keep the fish, watch them closely, then the best results may appear in the second, or later generations. This information I have mentioned a few times before but I certainly bears repeating. Success with guppies does not come overnight, or even in a year, except in cases of extreme luck, or a lot of skill.

If you as a breeder desire to add in a little gold stock to your own I suggest you watch local pet shops, Florida fish farms sell a lot of gold guppies, but seldom are these likely to look good, or be in the same category as show stock. These still can be useful to use as outcrosses as they usually are quite true-breeding for what they show.

One attribute about gold guppies that may not be fully realized. A gold guppy crossed to another gold guppy will give all golds. It does not matter how many times this same gold has been blended with grey guppies, he or she will still be true breeding for one thing — the gold coloration. Naturally, this can be mixed as to caudal or dorsal colors, or even with portions of the body being colored, but the background or body color will still be gold. The "gold" by the way comes in a variety of shades, ranging from near-white (blonde) to all shades of gold from pale gold to a deep butter yellow. In some strains, a litter of baby fish may show all color variations as described but it takes a sharp and possibly experienced one with good eyes to see the differences, especially in the baby guppies.

A line of grey guppies (red as one example I am familiar with) once crossed with golds will most always throw percentages of golds from then on — with these becoming more in evidence with close inbreeding. Generally speaking, the addition of coloring over the basic gold will be a variable but if at all possible use red-golds for use with red-grey guppies, green golds with green-grey, etc. Naturally, if you can only obtain a gold guppy of one color this is better than none at all and eventually, can be made into another color with the body gold.

The best practice with outcrossing is to keep a strain purebred that is found (by actual experience) to be compatible with your own. If tank space is at a premium, a single tank set up to just keep on hand some of the strain needed will be adequate. Even better, as stated many times before, is to find another breeder or set one up with guppies related to your own and swap fish at intervals. This can be made into a series of "linebreeding" methods, or just a way to allow someone else to work strains compatible to your own. If they can be kept reasonably purebred. The above article is not meant to be the ultimate answer to all guppy problems for everyone everywhere. It is just a series of suggestions that has been found to help.

Reprint: Fancy Guppy Correspondence Club, Feb 1971

NEW DEVELOPMENTS IN FANCY GUPPIES

by George McCusker

This is simply "make" or develop your own strains of guppies with what ever guppies that are available. If you think this statement is a bit "far-out", let me mention that I have been contacted by at least three people over the past year who mentioned that they are attempting to do this very thing. Add to this that I know of another three persons who are also doing the same thing and you can readily see that the idea is not too unique as it may sound. What even makes it more interesting is the fact that of the total of six people at I but one are working from breeding stock that is essentially little more than common guppies. There are good reasons for this and with a little thought, the idea makes some sense.

Whenever someone mentions that he would like to see someone come up with a new guppy type and attempts to describe what "new" is, I have to exercise a lot of patience. Given enough guppies to choose from, and the tank space to allow this to reasonably mature, I maintain that most any strain will eventually show up with fish that are essentially different from what is normal. But these are the very kind that a breeder wants no part of and the strangers are eliminated as soon as they are seen. I do not mean to imply that all of these fish are or should be further worked but just an attempt to show that if one uses some close observation, a little imagination, and one heck of a lot of patience, some of the strange guppies could be further developed into something new and very likely different.

Besides the actual attempts to breed different guppy types and colors, there is a little bit of pure research going on with guppies in an attempt to use the fish to find out something new — not necessarily directly affecting guppies. The use of guppies for carcinoma findings in one such, and in case this term is strange, it simply means the disease known as cancer. Most tropical fish can contract this disease and show the effects of it relatively quickly, or so I have been told. However, one must have some background training to work with such diseases and have the knowledge to know what he is doing while he is doing. Normally, a guppy breeder who has a strain of guppies that tend to show bumps, deformities, tumors, or odd bulges either eliminates the entire strain, or at the very worst, culls out the individuals showing the symptoms. In my entire experience, I have only heard of two individuals who are actively cultivating

guppies that tend toward cancer — one type or the other. One of these was a priest, the other a research technician who was the representative for a chemical supply house. As far as I know, all of their findings are secret or at least not available to the regular hobbyist.

In any attempts to create a new kind of guppy, it is neither quick, simple, or easy. Any observable progress takes years and the quickest I have ever seen any new guppy to be made true enough breeding was some five years in the making. Add to this that it takes lots of tanks, lots of breeding far area, and even worse no quick return in money, or fame. In my own opinion, most breeders think it far more profitable to concentrate their talent on making a better line of more likely winning show fish.

When it comes to answers to the specific question: What are the most wanted new kinds of fancy guppies? The answers seem to be quite standardized. The most commonly heard answer seems to be some color of "giant" guppy. When one further asks, what is actually meant by a four-inch male fish that would rival the moresena family. As far as I can determine, the giant guppy of today that is available at intervals would be about 2 - 2 1/2 inches in length, excluding tail.

Next heard, is the guppy that is entirely of a single color throughout the entire body. Black seems to be first choice with red second, and blue coming in third in the answers of any number.

If one insists on a third choice of the most likely fancy guppy that would be wanted, the answers become more vague but new combinations of existing colors seemingly a what is wanted. Such as red fins on a blue guppy, or black fins on a green guppy as some specific answers.

An interesting side light on these speculations, that a lot of the ones actually doing the experimenting with new guppy types seems to be the person who is isolated and is not sure what is available, being alone in other places, or having no access to knowledge that is already commonly accepted by areas having lots of guppy people.

Naturally, a breeder who has never seen a guppy show, never attended a guppy club meeting or one that is not even sure that he has really decent fancy guppies, usually has no idea of the complexities of attempting to develop a new strain. In fact, if he is lucky enough to get the facts all carefully laid out and explained in detail, he will actually think there is great exaggeration and will go on attempting the same thing he has been doing and think he is making great progress even when he is duplicating work done by someone else long ago in another area.

At this stage of guppy progress it is impossible to know how many promising guppy specimens have appeared in someone's tanks and have been lost due to lack of knowledge of what they were, lost by bad luck, or lost by plain old lack of knowledge of how best to handle them. Add to this the definite discouragement among so many people who know the work and time needed to make something useful out of a single fish and the picture becomes more gloomy at the time.

When mentioning guppy progress, I always like to throw in a few comments on color and the possibilities in this, not that anything new would be of interest that I have heard lately, but there is always room for more colorful guppies and improvement of the same colors in the ones seen around. One of the things that bothers me in this respect is the extreme variations in the same fish of the same color when he is changed to a different tank of a different breeder. Until now, I have tentatively blamed these changes on water, differences and I still tend to do so, but I am not sure this is correct or the ultimate answer. For example, "What makes a blue guppy, that has been blue for generations, turn green when he is moved across town? Or, on the other hand, a bright green guppy turns dark blue in just a few weeks when he is moved from his breeding tanks to a hard water area of a new owner a few hundred miles away? To

Complicate the problem even more, it is not at all unusual to see a strain of bright red guppies that I are very clear in the coloring, show up with lots of dark areas when they are shipped to another section of the country. These are all examples of speculations and while I certainly do not have a bona fide, complete & sure answer, the fact remains that the things do happen and if there are any sure answers, I have not seen them.

It is common to have a couple of guppy people sit up a "night" "talking" guppies. Or in some cases, an entire group of guppy people doing the same thing in a motel room someplace where they have gathered to enter a guppy show. If anyone reading this has been one of such a group, I think you will agree there is lots of pure speculation, but speculation about new and different guppies (as well as most other things) but seldom any sure answers. I have seen some guppy club meetings revert to back and forth comment on this same thing and while lots of opinions are heard, seldom are any new facts brought to light. One of the suggestions that come up at definite intervals in some method to artificially cause guppies to mutate, or to radically change by artificially attempting to alter the fishes make up either by combinations of chemicals, radiation (X-ray, radium or v.l. high-frequency radio waves), hormones or, just plain anything goes methods. While I am sure some of this has already been done, and more will likely be done sooner or later, the potential of these methods are not ones that seem able to do the job without a lot of bad side-effects such as being a quick way to eliminate a lot of good guppies, or to make such a batch of freaks, cripples, deformed and sterile fish as to give most anyone discouragement. I have no doubt but what someone will always bring up this topic wherever guppy people bandy about the progress being made (or not made) these days with guppies.

Add to the above the fact that variable, invisible and even the amount of light (either artificial or natural) has a definite effect on most fish, and especially so with fancy guppies, and you open up more pure discussion and a lot of impure speculation. While I do not mean to antagonize anyone, the fact remains that hobbyists have noticed long ago that certain things do influence the breeding of fancy guppies and some have even went so far as to attempt to prove what is doing it. I regret to say that what is shown to be the "rule" in one breeder's tanks, is not necessarily so in another's tanks. I have heard a number of times over the years that one man attributes his best strain of blue, green, gold or most any color of guppy to the fact that he is using a certain type of light, a certain number of hours per day. To even further complicate the matter, the expounder of this theory may be exactly correct — but only with his fish, and in his tanks with his methods. In my opinion, the overlooked facts of one man using salt, or rainwater, or formalin, or even partly filled tanks as compared to full filled, much deeper ones than the other breeder and may have a great influence, but how, why and how much, no one can say.

To sum it all up guppy people need, want and are actively seeking as well as speculating on new kinds and types of guppies, but on the whole this is nothing more nor less than the old trial and error methods that do come up with some success but slowly and unpredictably.

Reprint - The Fancy Guppy Correspondence Club - Feb 1976

LINE BREEDING

by Joseph L. Tuppler Jr

When the subject of line breeding is brought up, most fanciers regard it as the breeding of closely related fish which come from parents exhibiting desired traits. At most they will have some appreciation of the need periodically for crossing their strains with like fish from other fanciers.

There is more to it than this. Proper line breeding not only allows the breeder to maintain a desired strain and to fix new types which crop up, but also, if coupled with some knowledge of trait inheritance, to develop new strains or improve old ones.

Select the two best of your stock and breed them back to their parents, mother with son and father with daughter. This fixes your parental lines.

These two lines are not line bred with brother/sister crosses using the best pair from each successive generation for from four to five generations. How many inbred generations you can use without weakening your line depends on how robust your stock was to start with and what mutation rate you experience. Each generation must be culled ruthlessly to only a few pairs, and the best male and female mated for the next step.

After your line has been inbred for four or five generations, you select your best pair from of the two lines your original breeding gave you, and you cross between the lines, the male from one line with the female from the other, and the female from the first line with the male of the other.

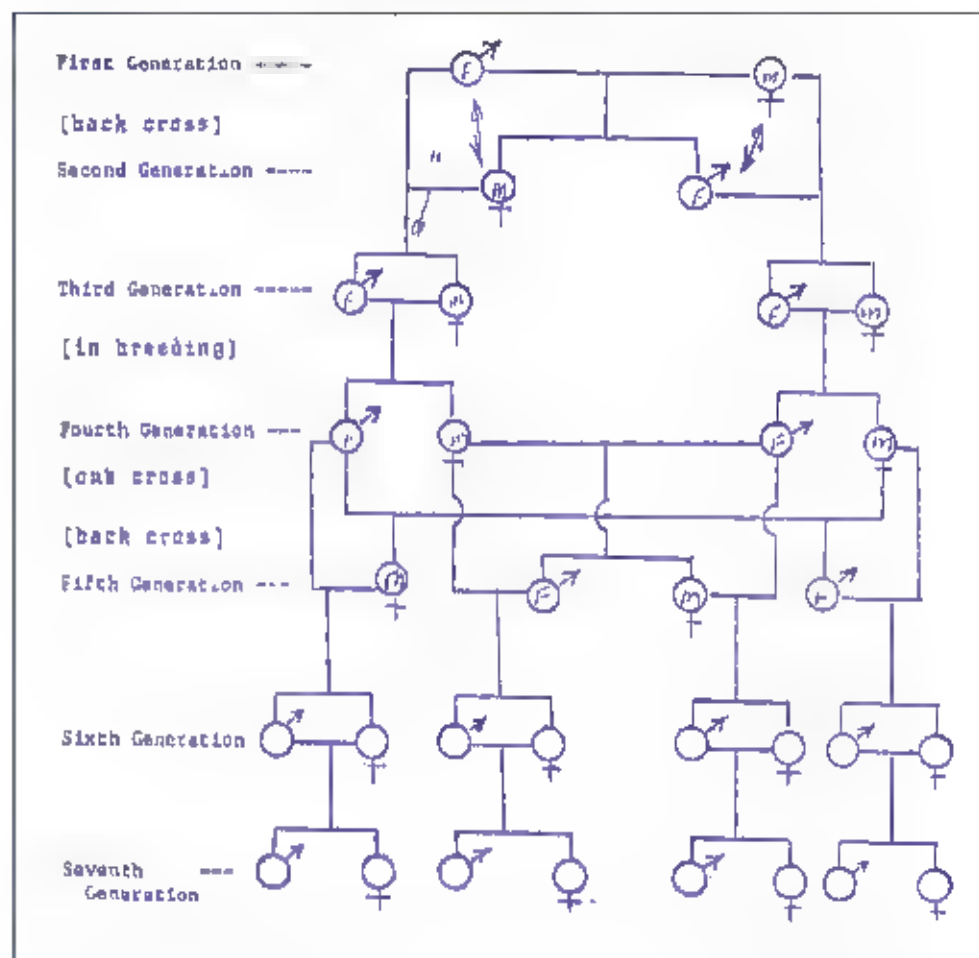
Again you conserve your breeders because following your outcross, you re-establish your lines by breeding mother/son and father/daughter on both sides of the cross. This will give you four lines. If you take the better line from each of your new uprisings and continue inbreeding with your new parental lines, this sequence can be continued indefinitely as in each unit of inbreeding you are building up a series of generations of fish which are only distantly related to each other. Each time you cross lines, it has the effect of bringing in unselected stock.

If you remember to select and cull, select, and cull and to maintain your parent lines for your crosses, you can improve your fish immensely in a few generations.

See diagram on next page

The diagram shows in simplified form the initial breeding and steps to fix the first two, and then four lines by backcrossing at appropriate points (i.e. mother/son, father/daughter), crossing and inbreeding (brother/sister) between lines.

LINE BREEDING DIAGRAM



The above are excerpt from an extensive article in the January, 1974 "Wet Pet Gazette" as reprinted in, "The Fish Tale", May-June 1974
For information about the original article contact
Davis Aquarium Society, P.O. Box 559 Davis, Calif. 95616,

INBREEDING GUPPIES

by Ronald Hood

Inbreeding does not cause bad characteristics in guppies. Many and probably all the ill effects attributed to inbreeding are not due to the inbreeding itself. The bad characteristics you may see in inbred fish were all there at the time you first started to inbreed the strain. The reason they show up so much more frequently subsequent to inbreeding is merely this: Most bad characteristics are recessive. That is to say (this is somewhat over simplified) if there are two genes for the characteristic, and one is recessive to the other, only the effect of the dominant gene will be expressed and will not be visible in the fish's appearance. Only when the individual is homozygous for the recessive gene (i.e., has two recessive genes and no other for the given trait) will the characteristic caused by the recessive gene be evident. The reason that most bad traits are due to recessive genes is that, if such a trait is due to a dominant gene, any fish that has at least one of the dominant genes would show the bad characteristic and be culled. This culls down on the fish with such traits. However, if the bad characteristics are due to a recessive gene, it can be passed from generation to generation without the breeder being able to tell in many cases whether a particular fish is carrier of the bad gene or not. For most traits of this type the only way to spot a carrier (a fish with one bad recessive gene for a particular trait) is:

1. Breed the fish to know carriers and see if any of the offspring are born as homozygous recessives.
2. Breed the fish to homozygous recessives (here, if the fish is a carrier, 1/2 of the offspring will display the trait; if the fish is not a carrier, none of the offspring will display the trait).
3. Breed the fish (this is only practical for males, to a number of its own offspring (if the fish in question is a carrier, half of its daughters will be carriers, and can be used for testing) and see if the bad trait appears.

Now, guppies are due to hidden recessive genes you will be much more likely to see these traits come out if you mate close relatives. That is because the chances that any two fish will both be carrying the same bad recessive gene become greater the more closely the fish are related. Widely unrelated strains may have many bad genes hidden in their genetic makeup, but they are not nearly so likely to have the same bad genes as fish from the same strain (which share the genes from common ancestors). This explains why people claim that an outcross miraculously eliminates all ill effects noted in inbred fish in one generation. In reality, the bad traits were not eliminated at all; they were merely masked by dominant genes.

As soon as the resultant offspring are mated to each other or back to either parent strain, the bad recessive genes start showing their effects again as they show up in the homozygous state in succeeding generations. The guppy breeder takes note of this and says, "Aha, it's all due to inbreeding!"

The guppy breeder can take advantage of the situation arising following inbreeding. As bad traits begin to show in the strain of fish, individuals showing these can be culled out. If sufficient numbers are used and culling is applied properly, undesirable defects can eventually be eliminated from a strain to a large extent. This does, however, require rearing large numbers of fish and culling very heavily. It also helps if the breeder knows something of the mode of inheritance for the traits he is trying to eliminate. It is desirable to start with the best fish possible, possessing the fewest possible undesirable traits and at least the major desirable traits one wishes to preserve. There are several different breeding plans which can be followed, depending on a number of factors, such as tank space available. It is desirable to try to inbreed

several lines at once from the original strain, keeping each line pure to itself. Each generation of inbreeding (i.e., mating only closely related individuals) will tend to decrease the number of certain genes in the population. This results in more and more homozygosity for each genetically determined trait. In other words, of all the possible genes for a given trait present in the original population, eventually after enough inbreeding, there will be only one kind left in the population for that trait. This particular variation of the trait resulting from the type of gene that is left in the population is then said to be fixed in the strain, and will never vary (although the expression in a given fish maybe altered somewhat by environment) unless there is a mutation of the gene in one of the individuals of the population. By a mutation, I mean an alteration of the gene so that it no longer causes the same trait as it did originally. Mutations are relatively rare, and most that do occur are of no consequence. However, a mutation can introduce variation into a homozygous population, even if infrequently.

The reason for trying to carry several inbred lines of the same strain is this. As the genes for each trait in a given line become homozygous, some bad characteristics are bound to be fixed in the lines along with the good ones, no matter how carefully you cull and select, trying to save only what you are looking for. Chances are good however, that the bad traits fixed in one line will not be the same as the ones fixed in another line. Then, after several generations of inbreeding, when you have fish that breed true for many of their characteristics, you can cross the separate lines to try to combine as many good things as possible in each fish. Then, take the most successful of such crosses and begin the whole inbreeding process again with several separate lines. Only if the strain becomes completely infertile or if a particular important desired trait is completely lost from all lines of the strain, should you need to outcross. Finally, when you have a strain that is true breeding for many desirable traits, and if you have not suffered a nervous breakdown in the interim, you can use this strain to outcross on any good strain of inbred guppies with excellent chances of producing really good looking fish. By no means outcross all of your inbreeds, though, because a good inbred strain is like "money in the bank" and certainly hard to come by.

Inbred guppies do tend to lose size and vigor for various reasons, and this is another reason it is important to breed as many fish in each generation as possible, because selecting the most vigorous and largest will tend to prevent such problems. I'd also like to mention that although many bad characteristics are recessive, that is not to say that all are, or that all good traits are dominant. Also, there are other modes of inheritance than simple dominant-recessive types. For example, some traits are due to a particular combination of genes that are not alike, and inbreeding eliminates this. Also, dominance is not always complete, so that a given dominant gene may not always completely mask the effect of another gene. I could go on at length, but the reader desiring more information can read books on elementary genetics. I have heard people say that guppies don't inherit their characteristics in the same way that other animals do, but this is also nonsense. Guppy genetics is complex, I'll admit, but in every case where the mode of inheritance for a guppy characteristic has been studied enough to work it out, it has been found to follow the same "laws" as are operative in other animals. I think the reason for the idea that guppies are different is lack of knowledge of just how complex the inheritance of a particular trait can be.

METHODS OF RESTRICTED GUPPY BREEDING

by George B. McCracken

This article is written for those persons who would like to breed good guppies but are handicapped in either the money line or have restricted space. I don't mean to say that it is likely that the methods given will attempt to compete with the breeders who keep great numbers of tanks and can choose breeding stock from hundreds of fish and several different strains. It is a method that has been modified to give a few guppies a reasonable quality and possibly a very few of an excellent quality. It differs from the better known ways of breeding fancy guppies only in the smaller size of the tanks used plus the means to take advantage of fewer tanks. Persons living in small apartments, mobile homes, and with limited funds can use these suggestions to breed fancy guppies.

RULE NUMBER ONE - NUMBER OF TANKS.

For any one kind or strain of guppies to be bred, at least three separate and individual tanks will be needed just to maintain the strain of guppies. If you desire to attempt the improving of these fish, as most of us do, you will have to add two more tanks to this number. Size is relatively unimportant to start. While 30-gallon tanks maybe desirable, five-gallon tanks will do provided you can be satisfied with smaller numbers of guppies. In extreme cases, even two-gallon tanks can be used to breed fancy guppies provided the extra time is available to clean them more often to sort (cull) out the young fish and to otherwise make for more nearly perfect conditions.

Filtering of the tanks is almost a necessity. The type of filter to be used is not important as long as some type is used. Without going into all methods of filtering aquariums, I would advise the consideration of bare bottom tanks to allow for easier cleaning, and to give the maximum in water space.

Another thing which is desirable but NOT absolutely necessary is enough light over your tanks to grow some type of plant. Some of the best guppies are raised without this feature but a few floating plants growing well does wonders in looks, provides havens for young and tired female fish and gives the fish natural conditions. Hornwort, nutia, watersprite, anacharis, and bladderwort all work well with guppies.

RULE NUMBER TWO - BREEDING STOCK

I well realize that good breeding stock is not easy or cheap to come by in certain parts of the United States. If this is one of your problems, look through the advertising section of any commercial aquarium publication and consider ordering your fish by mail-order. Do not attempt to order more than one color or kind at first. If red guppies are your favorite, stick with this one fish. You will have far too few tanks to do much good with several kinds no matter how big the temptation.

If you are one of the lucky ones and can go someplace and choose your fish, by all means, pick young fish. Never more than four months old and preferably get females already bred. An old wide tailed male guppy is fine to look at, not so good to breed with, especially after he has been moved several times from his original breeder. I much prefer some kind of baby guppies than no fish at all which is likely to happen if virgin female guppies are put in with old males. Another thing, two females are just about twice as good as one, so if you can afford a trio of guppies to start with, do so. Especially so if you must order your fish by mail-order.

The older strains of guppies are apt to be truer breeding and unless you have access to some of the special newer strains I would advise sticking to the reds, blues, or greens. At the start of any guppy breeding program the biggest handicaps to get fish true enough in breeding to make a fair start. Even the very best of fancy guppies that are available are apt to only breed 40% true and this becomes a real problem to start with. No matter the color of the fish chosen, you will have to concentrate on this one strain for up to about two years before you can attempt any branching out. There is only ONE exception to this rule and I'll describe it for those having an interest in this method.

Pick a breeder of fancy guppies, agree to buy his very best and truest breeding stock and pay the price. It will be high, probably in the neighborhood of \$25.00 per pair. Like these fish as breeders and with a little care, and by breeding the best of each litter to each other, you can get good guppies for approximately two years. Then it will be necessary to go back and buy new stock for breeding. This new stock can be either crossed back into your own, or used exactly as your first pair. Either way will give good fish again but be considerably less trouble than keeping and improving the strain by standardized methods. From a monetary standpoint it can be quite profitable. If you can sell your surplus fish or can win often enough at area shows to make it worthwhile. Many many people employ this method of raising fancy guppies and it can be done with few tanks and the minimum of effort. The only drawbacks are the cost in stock purchased and the availability of breeders who will sell you good breeding pairs.

For persons with limited space and facilities, it is impossible to breed good guppies and keep them good provided they compromise on quantity and make up for this by "exceptional care". This, combined with good breeding practices can give you guppies to compete with the best in one kind only.

RULE NUMBER THREE - BREEDING METHODS.

Some of the suggested rules given under this heading may sound very radical and harsh. They have to be or the restricted space you have will be less than useless. If you find that you cannot follow these suggestions, you can never successfully raise fancy guppies. It is as simple as that. Taking for granted that you have set aside five tanks for guppy propagation, follow these steps:

- (1) In one tank put your breeder pair or trio. Carefully record the date, the age of the fish if known and the source they were obtained from. Some do this by means of cards fastened to the tank front. Others keep file record. A few do both. I usually compromise and write with a felt tipped marker on the tank frame the dates and kinds of guppies concerned. Further information of a more detailed nature is on file cards. Remember all baby guppies look much alike and it is a long wait before you can see enough color in young males to guess what kind of guppies they maybe.
- (2) After the female guppy drops her young, remove the parent fish. Put the female into one tank, the male into another. You now have three tanks occupied, and two empty waiting tanks. As soon as you can, begin to sex the young guppies. Put the female fish with the old, female or into a new tank. The male fish go into the tank with the original male parent where they will stay until mature.

Here is where the hard part comes in. If this first litter of guppies was large, that is twenty-five fish or over, you now MUST discard all but three female fish and two male fish. Either give them away or flush them down the sewer. The biggest question is which are to be kept. This, at its very best, is a compromise situation and will be mostly guesswork in this final attempt. Pick the males for early coloration, brightness of color, and for vigor. Tail width is one thing that cannot be determined usually at this early stage. Later on

as you become more familiar with the strain, You can guess very close which fish are the exceptional ones.

Under the limitations, you should now have two young male guppies and three young virgin female guppies. These are probably of doubtful quality due to the first mating being of unknown parentage. The next litter of young is the important one and I would advise extreme care. From your records, you should have a good idea as to when the fry are due and several days before the 28th day, move the heavy female to the remaining (clean and empty) tank. If the tank is small, under five gallons, it is quite likely the female will try to eat her young as they drop. A heavily planted tank is better than a breeding trap, although either can be used. If large numbers of young are seen all well and good, but if the female is small you will need to try and save all the babies you can. Editor's Note: The author is assuming the purchased female was brought pregnant, as he suggested, so that the true father of the first litter is unknown. The assumption is also made that the second litter will be fathered by the purchased male. The latter assumption will only be true if the male is put with the female immediately after the first litter is born.

This (second) is the litter that your future breeding stock will come from and the bigger the selection to choose from, the better. As with the first litter, YOU can save only a small percentage of the total, while the rest have to be discarded. As soon as possible, pick out three virgin fish and add to the tank with the other three females from the first litter. Actually, you can breed your females while small, as you don't care too much for large numbers after the second dropping. About two months of age is OK or when the fish reach about one inch in body length. This is large enough to give 10 to 15 baby fish, which are still more than you can use.

What we are striving for is for one tank to be used for virgin females only, another five male guppies, and third with newest litter growing up to be sexed and a spare tank for the newest breeding attempt. This gives you one tank for either another breeding or to use for a litter of babies growing up. In practice, this maybe quite variable depending on your success with the original pair. Watch out for the overcrowding, one of the biggest drawbacks to this system. The only real cure for this is heavy "culling" of the young fish.

RULE NUMBER FOUR - EXCEPTIONAL CARE AND FEEDING.

The exceedingly complex nature of this subject is one that can only be briefly outlined in this article. In essence, it means giving your guppies the very best of perfect care. This is the only method that can make average guppies into exceptionally good ones. As soon as guppies are born, a program of heavy feeding is needed to give them the early start toward early maturing. The very best method to do this is to feed baby brine shrimp, but this has to be the basic diet for the first three weeks of the fishes' life. A once or twice a day feeding of a fine, powdered dry food helps but is apt to be ignored unless of high quality. If a "paste type" of food is available (some commercial firms make and sell this, most guppy breeders make their own), in between feedings of this does much to make guppies grow. Even a fish-styke of cat food will make excellent food for growing guppies if not overfed.

How much is too much in guppy feeding? Probably no one knows. Many feed as often as twelve times a day, even more under 24 hour lighting. Some commercial and semi-commercial people do this. If you have the time, or there is someone available throughout the day to do so, feed every two hours. A compromise is twice in the morning and three times in the afternoon and evening.

Under this amount of feeding, a stringent program of water siphoning and filter cleaning is necessary. If the time can be had, each and every tank should have 1/3 of the water changed weekly. This is done by using a small hose, siphoning water and debris from the tank bottom and then adding fresh water to fill.

the tank back up. After setting, the old water is excellent for brine shrimp hatching. In fact, it is better than newer water and gives both better hatches and will sustain baby shrimp for a day longer.

Without going too deeply into reasons, fresh water added to guppy tanks does a great deal toward making better guppies, other than the easily kept reason for a cleaner tank and cleaner water. About 5 to 8 guppies to a five-gallon tank is very good. If well filtered and maintained, 10 guppies can be kept, but this is almost too crowded to do the best with them. About two normal sized fish can be kept in a 2-1/2 or 3-1/2 gallon tank, but this can be stretched to 3 or 4. If at all possible, keep 3 smaller tanks and make the other two 7 or 10 gallon ones. In this way you can keep a larger litter of babies for the first three weeks before moving to the larger tanks and then transfer into the smaller tanks as the wide ones develop. Virgin female guppies gain size rather slowly. By breeding females relatively early, some strains give off fewer but better quality fish. It is hard to tell which is better among fancy guppies, the fish from the first or second litters. In most cases, one fish to breed and one kept as a spare is enough. Three virgin female guppies will cover for any eventualities. The extra fish if not used, can be traded for another good male from another breeder, which can give your fish a needed boost later on.

RULE NUMBER FIVE - FURTHER NOTES, HINTS AND HELPS

By keeping to a rigid planned schedule of maintaining the tanks, feeding well and often, by breeding only the best of your fish together there is no reason why you cannot have good guppies. As this article can only give the method and not so much the way to do it, you will have to get other standard books to find out the proper way to maintain your fish. Feeding methods and kinds of foods, the way to prepare and keep them, and the equipment necessary to do the best job are all well stated in many standard publications.

Certain things are a must in the breeding of fancy guppies. By choosing the largest, most colorful, and virgins of each generation to breed for the new generations, you will make great progress with your fish for up to 7 generations or longer. After this period of time, usually about two years, you will have to look around for a new male to breed into your fish, as it is best to get routed stock, try to obtain this new fish from the same source as the first pair. While it can be done, don't make the common mistake of breeding in another color to the fish you have been working with. Only gold or albino look well in doing this and they have problems of an entirely different nature.

By keeping male guppies in one single tank, by segregating the young virgin females, and by using the other three tanks for mating and for litters of young fish, you should be able to do very well. With time and experience, you will begin to see ways to further make better use of the available space. As an example, when adding new virgin females to the proper tank, they will be smaller than the ones now in it. Therefore, you should be able to distinguish them from the others on your records. As you must use the fish while they are still relatively small, there is no danger of the small ones catching up in growth with the larger, older fish.

Certain kinds of fancy guppies now available are easily distinguishable from other kinds even when mixed together. The 3/4 black guppies and the 3/4 black-red guppies are some of these strains. Even the females carry the black markings which makes them easy to carry together in the same tanks with other virgin females without danger getting the two mixed. Gold and albino guppies are others that can be carried along with the normal gray guppies with a minimum of extra tanks and related equipment being necessary.

There is one danger of using small tanks. Fancy guppies when bred and raised in confined areas tend not to get enough real exercise to be able to carry the large tails. They become "tail heavy" which means, it is likely to detract from their appearance. This means that sometimes it may be best to put a spare female fish into your tank of developing male fish to give them the needed exercise. This is also likely to happen with female guppies who are kept virgin too long. They get sluggish and hard to breed, so either breed them before this is likely to happen or destroy them.

Color is the first thing up to show poor in fish that have been inbred too long among themselves. When this appears, start considering new breeds to breed into your stock. If this is not done in time, body deformities are likely to begin to show in your fish.

In adding new water to your tanks for that lost by evaporation or by siphoning, it should be water that has "aged" for at least 24 hours. In small tanks this is especially important, but in tanks of ten gallons and larger tap water can usually be used.

Reprinted from GUPPY CHATTER by way of RAGGED TALES, Feb. 1974

CHOOSING BREEDERS

By Bob Fisher

Perhaps the most difficult problems facing any guppy breeder have to do with choosing the right breeders for future generations. Selection of the correct parents for the next generation is essential to maintain any existing strain, or to improve and build up a new strain. Many fish having good potential breeding qualities have been overlooked by beginners because they do not know precisely what to look for among their breeding stock in order to improve their strains.

There is no magic formula to insure success every time, but a few pointers on the subject may be of help.

When I started breeding guppies, I lost several promising strains by degeneration. I just didn't know what to do to preserve color, size or tail spread. So instead of improving, my fish gradually deteriorated until there was nothing left worth keeping. This sad experience has happened to most of us at some time or other, and looking back now, we are able to see the mistakes we made. My mistake was in breeding for color alone with not much thought to size or shape. Consequently, I soon had tanks full of beautifully colored midgets.

No one can accurately predict the outcome of a specific mating, but if we know the recent past history of the fish we are breeding, we can have a fair idea of what to expect.

Time is the biggest factor, because when we have committed ourselves to breed a specific pair of fish it takes about 3 or 4 months to have some idea of the outcome. If our choice of breeders was wrong, we have to start over again, but it is often too late, as the original breeding stock may no longer be around. So it is very important to use enough pairs to guarantee several batches of young from which to choose the best.

In choosing the male breeder, we pick out the male or male whose characteristics are highest - males with the largest size, widest tails, heaviest dorsals, brightest and purest colors, and most vigorous deportment. The qualities we are searching for may be present in only one fish or in several. These are the fish that should be carefully kept for breeding purposes. Each of these males should be examined for minor

defects and their pros and cons evaluated until the choice is narrowed to the few with the most promise. In the choice of breeders, observation is one of the most important factors. If in doubt, wait awhile longer to be really sure of your choice.

Having selected your male, you now need a female. It is my belief that this is the most difficult choice as there are only limited ways of finding what our gal can contribute to the mating. Past history of the strain is a good guide here. Color proving with hormones can be helpful, but can sterilize the female. About the best we can do is again eliminate by careful observation - selecting for size, shape, conformation, color and deportment. This still doesn't mean we've made the right choice, but we have narrowed the odds considerably.

As Peter Huter of Cleveland explains it, "In every hatch of fry there should be a male with the ability to improve the strain. He is usually quite easy to spot. Harder to spot is the female with the same ability. Therefore, it may at times be necessary to breed every female in a batch to find the right one."

When choosing the male breeder eliminate any having any slight spinal bends, thin narrow peduncles, uneven tails, dorsals not matching the tail, color pronounced wobbles in the swim, bloated or pinched bellies or droopy aft ends. Some of these defects are hereditary and some are caused by poor environment or diet, but none are desirable and breeder males should be healthy and vigorous. The same advice goes for the gals.

One up Pete Huter gave me. In choosing female breeders, go for those with short thick stubby bodies, wide peduncle regions, and wide tail spread. These females produce the widest tailed male offspring.

Of course, every strain of guppies is different. Jim Kelly of Eng and reports most success with superb tail females. I have better luck with round-tails. This is not to say that all females should be superb or round tails to produce wide tailed males, but to demonstrate that there is more than one way to skin a cat.

Remember, the goal of every guppy breeder is to originate and improve his own strain of fish. There is no short cut to success. Time and care taken in choosing the parents of the future generation pays large dividends. Lady Luck plays a part too, but the breeder is the controlling influence. And never try to raise every hatch to full maturity, rear only the very best.

NOTES: by Midge Hill - I firmly believe that to accurately control your breeding program females must be kept separate from the males until you can select the best to use as breeding. Although it is possible to use a non-virgin female and let the selected male take over for the next hatches of fry, there is absolutely no assurance that this has happened, nor does it always happen that the entire next hatch will be from this second male. And how do you tell which ones were from which male? The only way to be really sure is to work with virgin females only.

I am constantly surprised by breeders who claim their strains are pure enough that they can leave the males with the females and raising any resulting fry. I wonder just how long is before the beautifully large bodied, wide tailed, bright-colored strain starts to get smaller, have less finage and/or lose their bright colors. It makes sense to me, that to improve your strain you must breed from the very best fish, not the average. In addition to the more selective breeding possible with virgin females, females that have been kept virgin until about four months old almost invariably grow to be considerably larger than those bred at younger ages. However, at about four months of age they should be bred as after that age they tend to lose their fertility and become harder to impregnate, sometimes even becoming sterile. Reprinted and condensed from "Dherchez La Femme" by Bob Fisher of Toronto as printed in "Guppy News, Aug. 65 & San Gabriel Valley Guppy Association Nov., 67.

GUPPIES, FACT OR FANTASY

by Frank Doyes, San Diego, California

For many years, hobbyists such as I have accepted much of the information available in the subject of care and development of the broadtail guppies. It is time many of the old theories that years ago were thought applicable were closely examined. For example, the guppy breeders of times past would have been horrified at the current trend to change a considerable portion of the tank water weekly. I wonder what they would have thought, to observe my use of sometimes up to 75% of the water right out of the tap for the past 8 years or so.

The subject I wish to examine is genetics (?). As will be quickly observed by any of our astute writers, this is a topic which for practical purposes I know nothing about. I will beat one of the anonymous critics to the punch before he states once more that "obviously Mr. Doyes not only knows very little about modern guppies, showing them, or genetics." In the development of the broadtail guppy certainly close inbreeding was necessary, as it still is, to bring out a particular characteristic observed in a mutation or a cross. For years, I have accepted the theory that inbreeding was mandatory to maintain a superior line of guppies. Now it would be quite foolhardy of me not to agree with this, as I have had some small success with this practice. Continued inbreeding is excellent if it is done on a large scale, for example by one of the commercial breeders. When done on a large scale, the selection of breeders is made from thousands of guppies. If care is used in the selection, a strain could go on improving for many years. Unfortunately this does not hold true with the average hobbyist as he just does not have the selection of breeding stock to make the choice from. This perhaps explains why a hobbyist one year will make a big name for himself on the show circuit and fall flat on his face the next year. To continue his line, the simplest solution is to go back to his original source and obtain some breeders to cross with his present stock or to make an outcross with an equally good strain. For years I hesitated to make an outcross with my lines of guppies, one reason being assured by the many experts that when the first cross being superior due to hybrid vigor the second generation would really be junk. The other reason being that an equally suitable strain was not available here in San Diego and I did not make the effort to locate stock in other areas. Now that I am involved with several crosses I am particularly pleased with the results. The second generation young from these crosses also give indication of being very superior stock.

We read in the books how well guppies stand inbreeding and close inbreeding and accept this as a definite fact. I believe this to be just another of the old wave's tales. Now why should this be? It does not work with horses, sheep, hogs, or humans. What is the result of continued inbreeding and inbreeding on guppies? We all should know the answer: sterility, loss of vigor, color and most horrible, body distortions. It is disgusting to observe the number of grotesque shaped guppies in so many of the highly inbred strains and I regret to say that some of them show up in my tanks. Perhaps the most unfortunate fact is that this distortion sometime's does not occur until the guppy is from 4 to 5 months old, maybe after having young. I do not believe that this humpback and body distortion problem can be simply explained as hereditary but rather is due to weakness from continued inbreeding. In several instances in this area, the cross of two lines showing remarkable few examples of distortion.

We have charts showing in detail the dominant and recessive characteristics of guppies. These charts are just great, but the question I would like to ask is, where do we get the pure parents to work with? Why, in so many cases, is what should be a recessive characteristic in one particular strain of guppy, a dominant characteristic in another? It appears to me as mixed up as the average strains of guppies are, that very few conclusions can be made on guppy genetics. My observations seem to indicate that certain characteristics are dominant in some strains, while they are recessive in others.

To much credulity is given to a genetic chart obtained by a mixed amount of tests on one particular strain of guppies. The other trend is to show a genetic chart in great detail and then in small print, the word "theoretical." An article showing a genetic chart to have any meaning should show in detail how the results were obtained and not as so often is done, by researching another article which like us not came off the top of some one's head.

With the great number of hobbyists working with, for example, new guppies, to develop a stock to the AGA standards, I can't for the life of me, see why many of these lines are not compatible for crossing. The young from these crosses certainly in many cases will still be superior guppies. The combining of several, unused strains of guppies should result in renewed vigor and I believe eventually, superior guppies. This seems a more practical approach than the continued use of in-bred strains to produce hybrid guppies with the young unsatisfactory as breeders.

One point that has puzzled me in the Illustration in the AGA Standards. Why is the delta and ventral male shown with about 2/3 of the caudal fin below the center line of the caudal peduncle? This is very apparent if a line is projected along the top of the caudal peduncle through the tail fin and also along the bottom line. This would indicate that a bottom-heavy fin is desirable and would explain why so many guppies cannot carry the tail properly. It is simple mechanics to see that an unreasonable strain is placed on the caudal peduncle if 2/3 of the tail is below the center line. A guppy with an undersized caudal peduncle certainly cannot support the large finage required on show stock. To support a large caudal, the male guppy's tail should be shaped similarly to the fin on a wide tail female guppy. The caudal peduncle should be wide and extend well back into the tail. This overlapping results in the tail being well braced and allows the tail to be carried in an upright position. This tends to give a drooping tailed guppy. This type of tail allows the male to utilize the tail for propulsion instead of the entire job having to be done with the pectoral fins. It also explains the side vibration of the body necessary for small bodied, large tailed guppies to swim. Observe the ease with which a female guppy with a large tail fin can swim, with no side motion.

Reprinted from July, 1966 Tropical Breeze, San Diego, Calif.

VARIETY IN GUPPIES WHEN SPACE IS LIMITED

by Midge Hur

Most guppy breeders love variety...this is usually why they pick guppies in the first place, but raising a large variety of different types properly takes a great many tanks and a lot of space. It is simple to fill 9 tanks with just the offspring of one particular kind of guppy, but if you like variety it is possible to properly work and improve as many as 7 different kinds of guppies in those same 9 tanks by use of the following breeding program.

NOTE: I DID NOT SAY 7 PURE STRAINS! This "short cut" technique is not to be confused with maintaining pure strains (for which there is no really successful short cut of which I know). You will eventually end up with your own pure strains if the program is followed throughout, but in the beginning this is strictly a creative technique, which in itself can be very satisfying...a way to expand without adding more tanks.

For the sake of illustration, let's assume that our guppy raising space is limited to 9 tanks (5 gal or larger). The first step is to decide what basic color you prefer. Then comes the most important step of the whole breeding program...one which will decide the success or failure of all your efforts...the selection of the BASIC pure strain which will be behind all of the other variants in the 9-tank program. Don't scrimp here...shop around, talk to breeders, learn as much as possible about each strain, then purchase the VERY

BEST, truest-breeding strain you can find in the desired basic color...hopefully one that also carries a recessive trait such as gold, bronze or albino body color.

This becomes your BASIC strain. Breed the new strain immediately and when young are dropped, remove mom and dad to a holding tank. No attempt will be made to save their future litters unless tragedy strikes the first litter.

When fry are old enough, be sure to separate males from females IN TIME. This is vital as these young females will be the backbone of all other varieties in the program and will be the only females we will work with at all.

While these basic strain fry are growing in tanks #1 & 2, start looking around for other fish with which to start the variety part of the program. A little knowledge of genetics helps here as most of our varieties will utilize dominant characteristics which are visible in EACH generation. Most varieties of cobra or snakeskin patterns are carried on the Y chromosome and will therefore be passed directly from father to all of his sons. Some varieties of 3/4 black carry the trait on the Y chromosome and would be ideal for one of our varieties. If carried on the X chromosome they can still be used but require slightly different crossing methods and will only produce 50% males of the desired 3/4 black variety (except possibly in the initial cross) when bred in accordance with our program.

If the basic strain carries recessive, for gold, bronze, or a bino we do not need to seek an outside male with these characteristics as we can use a male from the basic strain with which to work this variant. We can also use a color variant, which will often throw multi-color fish when crossed into our different color.

For the sake of illustration, we will select a cobra, a Y-linked 3/4 black and a good fish of a different color than our basic strain (which we will say readily carries a recessive for gold). From these three plus the basic strain we can make in only 9 tanks 7 distinct varieties of guppies that will be true breeding for their variant characteristic...and in time all will be pure strains.

The program can be started when the basic strain F-1 females in tank 2 reach breeding age (about 3-4 months) and will be set up as follows:

Tank 1: Basic strain males, first litter

Tank 2: Basic strain virgin females from first litter

Tank 3: Cobra. (The selected 3/4 black male, 3 gray-bodied and at least 1 gold-bodied virgin basic strain female from tank 2)

Tank 4: 3/4 Black. (The selected 3/4 black male, 3 gray-bodied and at least 1 gold-bodied virgin basic strain female from tank 2)

Tank 5: Gold (or bronze or albino). Select the most promising gold male from tank #1 & add 2 or 3 gold females from tank 2.

Tank 6: Gold cobra (first litter will be gray-bodied cobras, all hybrid for gold). When gold females bred in tank 3 show signs of pregnancy remove to tank 6 for delivery.

Tank 7: Gold 3/4 Black (first litter will be gray-bodied hybrids). When gold females bred in tank 4 show signs of pregnancy, remove to tank 7 for delivery.

Tank 8: Multi (or some form of color variant). Put select male of any color different from basic strain color with 3 virgin basic strain females from tank 2.

Tank 9: Holding tank for mature males to show, sell or for emergency. (In case of X-linked 3/4 black, the process should be reversed. If a virgin female of the 3/4 black strain is available she is put into tank 4 with the best young basic strain male from tank 1. If no virgin female is available, put X-linked 3/4 black and breeding plan will remain reversed...basic strain Male to 3/4 black FEMALE for each new generation. Only 50% of males will be 3/4 black...it would pay to look for a Y-linked 3/4 black when breeding according to this program!

When females in tanks 1 through 8 are well loaded, remove males to tank 9. After fry are dropped remove and discard females. Sex fry as soon as possible and DISCARD all females except gold females in tank 5 which should be added to tank 2 to increase the supply of basic strain gold females with which to work. As young males begin to color up start discarding any that show undesirable characteristics. As they mature, gradually weed out all but the best. While they are maturing we will turn our attention back to the basic strain, which should be kept moving along and improving also. Being at least three months ahead of the variants, we can now select the very best male in tank 1 and remove at least 3 of the next best to tank 9 (in case of emergency). Select the best three females from tank 2 and put with the male in tank 1. When fry are dropped, continue as before. Discard parent females, sex fry, remove young virgin females to tank 2 discarding and of the gray-bodied F- females which might still remain. At this point, all good females are kept to insure a good supply for the breeding program as some times gold and albino females prove difficult or difficult or impossible to breed and new females must be bred.

As the breeding program continues, it may become obvious that one or more of the outcrosses are incompatible with the basic strain and do not produce good fish. In some cases this can be overcome by merely carrying the breed on for a few more generations, backcrossing to the basic strain females each time. In other cases it might prove best to recross a different strain of the variant involved and return the program for that variant. In the case of the fish in tank 5 (the gold, bronze or albino) it would be advisable every so often to breed the select male to a gray-bodied female of the basic strain to create stronger fish. (The gray-bodied fry from this breeding would be hybrid for gold and will produce 50% gold in the next generation when again bred to a gold female, and the gold variant is off and running again with new vigor).

It also may very well happen that the males in tank 8, when repeatedly crossed back to the basic strain, will gradually show higher and higher percentages of fish the basic strain coloration rather than the desired variant. If the fish are very high quality it would be advisable to procure another male from the same outcross strain to restart this variant. If the fish are good quality but not outstanding, why not try outcrossing to a different strain which differs in color from the basic strain and begin this portion of the breeding program again with the new variant.

As the BASIC strain guppies are kept as pure a strain, this breeding program is very flexible and any of the variants can be changed or deleted without affecting the other portions of the program. It also follows that the basic strain must be good and be carefully worked or the entire program will suffer.

If, by chance, you should find more room for additional tanks, more basic pure strains can be setup. Just think of the variations that could then be developed and systematically worked!

WHY YOU CANNOT RAISE A GOOD SHOW GUPPY

by Bob Maxwell

So Jersey Guppy Group

ONE - LACK OF AUTHORITATIVE INFORMATION

Perhaps the most misunderstood species of tropical fish that the hobbyist of today can get involved with is the guppy. If indeed you, as either an accomplished aquarist or as a complete novice in this avocation, ever meet a breeder who suggests that raising good quality guppies with any degree of consistency is an easy task and not worthy of the challenge, then be aware that this is a fool's paradise and you have just met one.

The guppy of today presents a real challenge to all of us, novice and breeder alike. Even though we might have a strain well established in our tanks, it is difficult enough to maintain it, let alone improve upon it. The guppy we read about in literature readily available today is a fascinating creature indeed. If we are to believe the books available on the subject we find that it is a species that

- 1 Can be raised by anyone
- 2 Can be housed in anything from a drainage ditch to the elaborate decorated tank in our living room
- 3 Can be fed anything from table scraps to "especially prepared diets"
- 4 Will breed and reproduce itself every 22-30 days and present us with multitudes of young so fast that we won't know what to do with all of them.

Unfortunately these bits of information are so far removed from the truth, so outdated, that many prospective hobbyists upon by the wayside in frustration when things go wrong in their tanks. If we make one point clear, it must be that the guppy of today is anything but the guppy we read about and find illustrated in the currently available literature.

While we must give proper credit and respect to the accomplished breeders of yesteryear, it is the writer's contention, that the guppy we are presently working with is far advanced from the guppy they were working with. If we take the time to compare the writings of the old timers, do we not notice the multitude of inconsistencies in their techniques? If we are to successfully follow in the footsteps of breeders such as Haniel, Samp, Mark, Hutter, and so many others who have left their mark on the hobby - the very least we need to work with is up to date and viable information.

Some points to consider when suddenly things go wrong in your tank and the answers are not to be found in your reference books are as follows:

- 1 The guppy of today is some 40 to 100 generations away from the guppy of your reference books. We cannot hope to estimate the number of genetic freaks and mutations that have taken place in these generations. Even the accomplished and respected geneticists of today are, at odds on many facets of guppy breeding and heredity. So much so, that the hobbyist that studies those writings is perhaps the worst off for even trying to make his breeding program from the results of the works of others.
- 2 Equipment and accessories available for your aquaria are much more scientific than what was available ten to twenty years ago. The manufacturers are at long last giving some real attention to the proper equipment, filtration systems, medicinal products and yes, even the tanks themselves. Advances in these areas have been great in the past couple of years and no doubt we will see greater strides in the future.

Now that we have you completely mixed up, telling you that the data you find in the books is probably all wrong, or at least out-of-date, where do you turn for information? The answers are, quite simple, in that you need to join and become active in an active club which is either devoted to the guppy entirely or has an established guppy group working within its ranks. Here you will be able to meet with ask questions of and generally pick the minds of other breeders who are spending their time and efforts on the guppy. The chances are that there is one or more members who have experienced the same problems that are troubling you and that they have the answers to your particular questions. Perhaps they may not have a solution that will work every time, but at least they can point you on the right track so that with a little effort you yourself will come up with the answer.

TWO - LACK OF PATIENCE

Perhaps the most important facet of any program planned to produce a top quality show guppy is patience. Each and every step in your breeding program can be carried out with well-planned precision, but the fact remains that either the development of the new strain or the maintenance of an established strain requires a considerable amount of documentation, tank maintenance, culling of stock, food preparation, selection of future breeders, etc. All of this simply means that without the willingness on your part to devote the hours necessary to accomplish your goal you are faced with a losing proposition.

Normal development and growth of a good show guppy (adult show size) will take some nine to twelve months. This means that you will not be able to actually select the best fish from a batch of fry for sometime, usually some six to eight months after birth. The breeder with the five months of age, after he is well acquainted with the strain and knows its various characteristics during its early development stages. The unknown breeder, however, must take additional time and wait further growth before he can make his actual selections.

All often we find that the novice breeder is making his breeding selections in a manner which is entirely wrong if he is in turn attempting to raise a large, show-type guppy. Rather than making his selection from the late developing males, he is picking those who show their color and develop their finage at an early age. This is fine if his goal is to raise a commercial type fish that will be saleable to sell at a local pet show or aquarium store at some four to six months of age. However, if he is truly attempting to develop a show guppy, this fish will not be attaining full maturity until it is from eight to twelve months of age.

The writer has observed more than one hobbyist who has gone out of his way to obtain breeding stock from a breeder of some reputation. The normal result is that he finds that the offspring from his breeders are much slower to grow than anything he has ever had before. Quite possibly the fry show little if any color even at three to four months of age and the unknown breeder simply throws them out thinking that they won't really develop into anything. Yet, with the true show-type strain, this is exactly what he should be looking for.

AGAIN PATIENCE IS THE ANSWER. TAKE THE TIME TO:

1. Search out the strain you want; talk to and visit every known breeder you can find.
2. Listen to and attempt to absorb every scrap of information you are able to glean from his answers to your questions.
3. Keep in touch with them periodically and give reports of your progress as well as your failures. He can and will generally be more than willing to make suggestions that can be of immense assistance in your program.
4. Last, but most important **BE PATIENT**. Remember, whatever strain you are working with

represents some forty to fifty years of selective breeding by other hobbyists and breeders. YOU cannot make any significant improvement in it over night. It may take you some four to five years to make any noticeable change from what you started with.

Without the patience and fortitude to carry your breeding program out to its final conclusion, you will seldom be listed amongst the winners at the end of any show.

Reprinted from the "South Jersey Tropical Fish Association

Publication" October and December 1974,

THE BEST IS IN THERE SOMEWHERE

by John Wolcott

In many instances we hear from the experienced, as well as the inexperienced, guppy breeder, about the rise of "Junk" he or she has received. Was it really the sender that sent the "junk" or was it the receiver that developed the "junk"?

If a breeder has a good strain of guppies, and someone orders or is given a trio from that strain, it only seems logical the new owner should be able to breed similar good guppies. It is hard to believe that someone would be good at selecting out only poor guppies for the owner.

Let's review what happens to the guppy from the beginning. Here are some Fancy Guppies swimming about in a nice roomy tank, water seems real good, fed regularly, lights just about right and temperature real cozy, but out of nowhere a net dips into this nice home and out comes two or three of the young fish. These guppies really didn't have a mobility program mapped out for themselves. From here on these guppies are in for quite a change. First into a container, then into a small plastic bag, turned upside down and then into a second plastic bag, placed into a small dark box and then bounced around in different temperatures for the next couple of days. Again placed into a container with someone pouring completely different water over them, and finally placed into a new home.

From here on the new owner, if he or she is careful, can produce good fancy guppies similar to those of the previous owner. The first important factor is the introduction of the guppies to the new water. This should be relatively slow, being careful with water conditions, (pH and temperature). Pour the fish and a lot of the water from the tank you previously set up to be their new home. This should take a few hours, add about a half cup at 30 minute intervals to ease the shock of the water change.

If all goes well, within a couple of weeks some fry should show up. When the fry are born the actual feeding becomes the second most important factor, small amounts of live food twice a day with dry food feedings spaced between will give the fry an excellent start. Continue with a good feeding schedule during their young life.

As the fry grow, a third important factor, "culling" should be started as soon as possible (unformed fish only). If space permits, males and females should be separated. If space is critical, culling should continue until only the very best (?) guppies remain. It is possible, when guppies are all left together that the poor males will mate with the better females, and the strain can start downhill from the very beginning. Culling out the smaller fish, the misshaped or deformed fish immediately will give your new strain a greater opportunity to produce good fish. Although many good fish will come from a drop of fry, only a very few will normally reach the show bench. As you work with the strain you can improve the proportion.

After about two months, the best two or three males and five or six females should be selected as your breeders. As the young from your selected breeders reach the age of six months, your guppies should start IFGA EXTRACTS Volume 1...July 1985 p 43

to look similar to those you saw some 10 to 12 months before. I believe it takes anywhere from .2 to .8 months to really give your new pair or trio of guppies a good chance to prove themselves. When you think of 11, 12, .8 months is quite some time, and time requires a lot of patience. However, if that strain of guppies caught your fancy, time should be a minor problem.

*(Imprinted from the Official Bulletin April 1975 of the International WtW Guppy Association
9903 Cuddle Drive, Whittier, California 90603)*

SELECTING BREEDERS

by Elvis Bryant

Before we go into details in breeding, let me straighten the misconception that people in general have about guppies. Guppies, you just put 5 males and 5 females and let nature take its course! Well, nothing can be further from the truth. No one can breed good guppies this way; there is too much chance that some will be bad, and, of course, nobody can predict a certain female's offspring in advance.

The most positive way to select breeders is to first determine what you want. Is it size, color, or both? One way may bring color but will lack size; another way may increase body size but lose color. Now you have taken that step, you want size and color together.

Male first. I watch the caudal region, what I want first in a male caudal. I watch all my males for a good (60) degree spread. Next I want my male to be a good solid in the caudal region. Next **BODY** size. I select the largest body size with all the requirements I desire in the two steps mentioned above.

You may have males with all the factors. In most cases good guppy breeders will have a dozen males to select from, but try to cull these down to two.

Females are very difficult to select. Carefully watch the females for color in the caudal area.

A Caudal region in the cauda is most desirable for blotches of mixed colors can be a lot of trouble. Next size of caudal. Pick a female with a nice high-swept caudal.

Next the membrane, (**PELID** **NO** **CL**) this is the region before the cauda, pick your female because of a thick membrane in this area. The thick membrane will help the offspring males to hold their large cauda.

SHAPE • Be especially careful for shape. This can be dangerous if you pick a female with a crooked spine. Sometimes an overhead view is best to determine this. A strong light to view these areas is always helpful. If you waste six months breeding only to find you used a female that had a crooked spine you may be a little mad.

SIZE • If you have cleared the three areas covered, you now can look for the largest female with all the characteristics mentioned before.

TRIOS, one male, two females are the best. I believe control is the best answer for using a trio. When the females are beginning to fill up with rise, separate them. You are better able to determine the quality of the young. Be sure to label each to tell months later from which female the young came. You may have a regret if all the young are mixed.

A young female may not have many young at first, but as she matures the amount of young will increase. By young I mean 4 to 6 months old. An older female does not mean better young. In fact, it is found to be opposite. Then after three groups of young, you will find it best not to take any more young from this female as she would be past her prime age.

INBREEDING - FACT AND FICTION

by Jack Rosengarten

Many things have been said about the evils of inbreeding but little seems to have been said about the true facts. Inbreeding can be either good or bad, or both, depending on the intent of the breeder and a certain element of luck.

Simply defined, inbreeding is the mating of closely related individuals. This has the effect of allowing recessive characteristics, which normally would stay hidden, to be displayed. Closely related individuals can be expected to be carrying the same recessive genes, and therefore some offspring will receive a pair of genes, which is what it takes to display a recessive characteristic.

Inbreeding, or incest as it is called when applied to humans, is frowned upon by society because of the well-documented occurrences of hereditary diseases in such relationships. Horse, cattle, dog and cat breeders avoid inbreeding for the same reasons. Many fish breeders think the same way, but should they?

Inbreeding concentrates all the recessive genes, the good and the bad. What then is different about inbreeding of the higher animals and fish? In a word, **NUMBERS**. Horses and cattle usually have one baby at a time. If an undesirable result occurs, it is costly and time consuming. Dogs and cats also have small litters so that inbreeding is a chancey. Fish, however, have large litters which yield a close approximation of the hereditary ratios developed by Mendel. Inbreeding does not create deformities. It merely makes it more possible for them to be displayed. Likewise, those longer fins, purer colors and greater size can also come to the forefront, instead of staying hidden. With large litters the breeder is not faced with a total loss of something goes wrong. In fact, he can expect something to go wrong and he can expect something to go right. That is where culling is important. A good breeder will select the next pair to breed very carefully. If he is lucky enough to have a lot of tanks, he should select a number of pairs so that all will not be lost if one wrong choice is made.

Many breeders will use schemes to provide insurance against running into a dead end. Either by using a crisscrossing method or inbreeding separate lines of the same strain. Some will combine both methods by crossing the lines after some number of generations. For breeding show male guppies, I prefer the breeding with as many pairings as possible since the females can truly only be selected by trial and error or at best an educated guess.

Records are important so that the breeder will know when something is going wrong. Ignoring the first indication of something going wrong, indiscriminate inbreeding, or population breeding where the true parents cannot be determined are the common pitfalls of a poor breeding program. Numerical counts of the good and bad results will let you know if the goals are being achieved. Merely culling every time a defect is spotted, without recording the fact, is living in a fool's paradise. This is the reason many breeders show spectacular results for a year or two and then lose their strain.

What should you do if a strain is deteriorating? Most breeders will dump them and buy some new stock from someone who knows what they are doing, and start all over again. What a waste! Breed your strain to a closely related strain and with a carefully determined method of selection continue to inbreed after this first cross, or if necessary do a second cross. Crosses increase vigor and all-around development, while inbreeding depletes these qualities after several generations.

SEPARATE QUARTERS

by Stan Shubel, Michigan Guppy Breeders

Like many other guppy people I simply do not have enough tanks for the number of lines I am trying to raise. At the present time I am running four lines of blues, three lines of reds, three lines of half-black reds and a line of purples - all in 54 tanks. With some simple arithmetic you can see I don't have a lot of available space per line. In a way I'm more fortunate than most in that my strains throw a very high percentage of good fish so it is not necessary to raise a large number of fish to get good show and breeding stock. Also I can combine males and females in separate tanks of similar age groups of the different color lines.

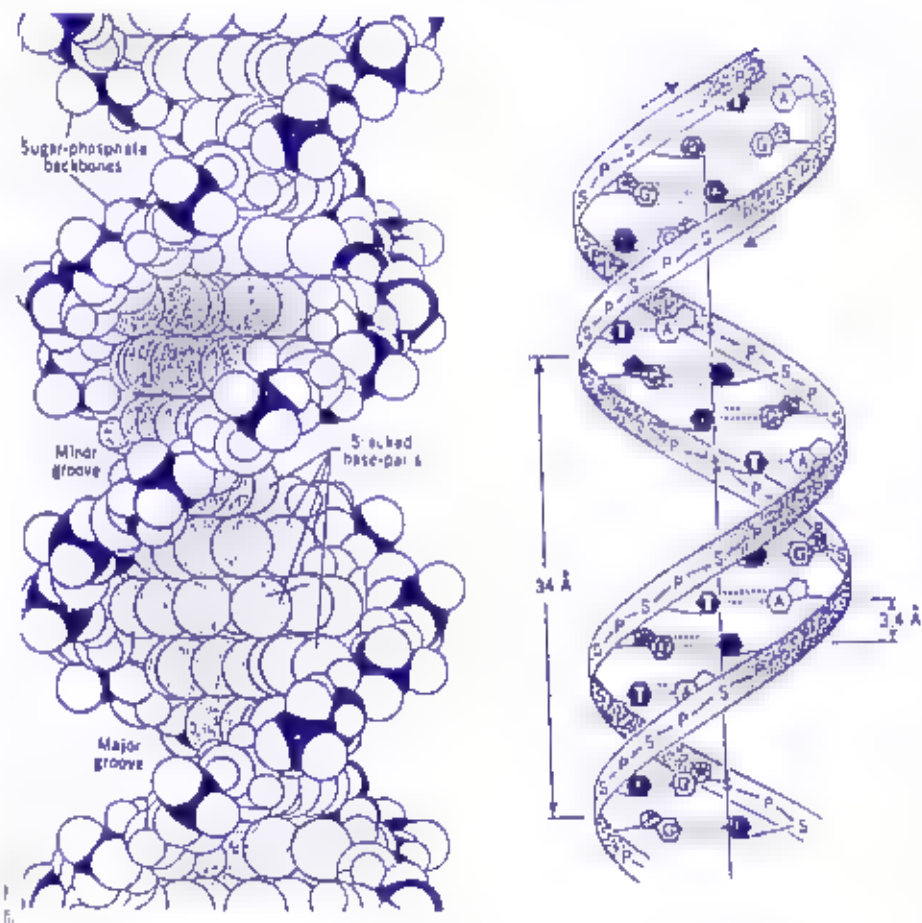
Even so, about a year ago, I ran out of space to set up some new breeders. It had been a common practice to isolate females about to drop young in a half gallon show jar to avoid harassment from her tank mates. So I thought - What the heck, and placed the trio into a spare jar. Initially I planned for this to be a temporary arrangement until a small tank became available. After a month or so went by the fish were doing fine, each of the females had dropped young and the male was swimming well. Shortly after this, I picked up a couple one gallon drum bowls and the fish were transferred to the larger bowl. Some more breeders were set up in other bowls.

The feeding of these fish was the same as for all my other fish. Live baby brine, my blended dry food and adult frozen brine shrimp. As no filtration or aeration was used, care was taken not to over feed. The water was changed every other week. The fish were netted out and placed in another jar until their own could be scrubbed down. Water was taken directly from an established tank. Nothing else was added to the water in the way of medication, salt, etc.

The original male is now over 20 months old and still going strong - one of the females just dropped young again. The caudal on all the males have held up remarkably well with no splitting or discoloration problems and the females have done as well. The only negative factor I can determine is that there has been no increase in body size. On the other hand, fish of the same lines left in the tanks with filtration and perhaps increased food supplies did continue to grow. But also sexual determination was a factor in the tanks. But to come to a definite conclusion would take a whole bunch of bowls over a longer period of time. Which I am not inclined to pursue as I am only interested in the practical aspects.

One additional benefit is that in the smaller area the bigger males are able to catch the females easier. This enables you to breed the older males without any trimming of the fins. But I did definitely prove that it is possible to maintain - you'll note I did not say raise fish in a small container with no outside air supply or filtration. So if you do run short of tank space it would seem that the drum bowls are an acceptable substitute.

GUPPY GENETICS



GENETICS AND BREEDING

A series of articles

by Dr. Joshua H. Wilson

INTRODUCTION

One of the most interesting developments of the twentieth century has been the clarification of the basic principles underlying the production of characteristics, or traits, in successive generations of living organisms. Although from time immemorial man has the causes of variation, it is only in comparatively recent years that any real understanding of the principles involved has been reached.

One of our routine observations is that cats give birth to cats. Cats have been up to this for centuries all the world over. Furthermore, there is no documented instance of a cat giving birth to anything else. This is the primary observation of the science of heredity.

By simple observations, one can conclude that Douglas firs produce seed that germinate to give only Douglas firs. The fruit fly, *Drosophila*, has been watched by the geneticists since 1910; and it has never given birth to anything other than *Drosophila*. Cats and firs are likewise the object of genetic research. They are prettier than flies but they share two major disadvantages as objects of study. They are big requiring lots of space and they are slow to reproduce, requiring lots of time.

The most elementary observation will provide us with material for thought along these lines. Dogs, for example, produce puppies, never kittens, yet the puppies in a litter may possess individuality that a child can distinguish one from the others by looking at it or by listening to a squeal or even by touching it in the dark. The puppies themselves will be able to distinguish any person from any other by odor as well as in other ways.

These familiar creatures possess in common another feature—their developmental cycles are sufficiently complicated that an analysis of their heredity requires a simultaneous understanding of all the basic principles of genetics.

No two individuals are exactly alike. Variability is a fundamental characteristic of living things. Although no two individuals are quite alike, we do recognize many similarities among organisms, and we soon come to realize that many of these similarities are obviously correlated with the closeness of the biological relationship between the individuals. We do not always so readily realize what is equally true, namely that the differences among individuals may also be correlated with the relationship between them.

Biological relationship, however, is only part of the cause of similarities and differences between individuals. Actually such individuality is the result of the interaction hereditary and environmental influences. The relative contribution of each of these influences vary from trait to trait and from circumstance to circumstance. The science of genetics embodies the study of the proportionate extent of the contributions of biological makeup and environment and the analysis of the principles and laws underlying the action of biological influences.

As a subject for thought and discussion, genetics arouses our keenest interest because we ourselves are the products of innumerable hereditary traits, developing and interacting under the influence of the environment which is our world. As a science genetics is subject to certain natural laws, and although relatively young it already compares in exactness with such older sciences as physics and chemistry.

While the basic principles of genetics are few and simple, I will attempt to present them with enough description of accessory areas to allow comprehension not only of the principles themselves but also of the

types of experiments from which the concepts have evolved. Such an approach compels the reader to ask: What is the evidence for this concept? What are its limitations? What are its applications?

The processes by which higher plants and animals arrive at their adulthood give striking testimony that living things conform to regular patterns. Consider that, for a given individual, life begins as a single fertilized egg cell. This cell multiplies, and its derivative cells redivide, aggregate, differentiate—all in a most remarkable and well-integrated manner—until the mature form characteristic of the adult organism is reached. Usually, the adult produces reproductive cells, either eggs or sperm. These unite with corresponding cells from a member of the opposite sex. Repeating the developmental stages of the generation before, such cells give rise eventually to new adults. Since life as we know it comes only from preexisting life, each individual is a member of a series which, generation after generation, passes through indefinite time.

It is apparent that there must be governing principles that regulate the continuity of individual life forms. The complex embryonic foldings, the growth, and the differentiation of development can in no sense be events occurring at random. They require unusually precise, cogeneration in time and space if the normal life cycle is to be completed.

One way of demonstrating the precision of this coordination is to disrupt it and observe the consequences. In laboratory experiments the regular sequence in the development of an individual can sometimes be slowed or arrested, for example, by so simple an agent as low temperature, or by changing the chemical environment of the embryo. A one-eye form of the Atlantic Coast minnow may be produced when eggs of this fish are permitted to develop in sea water to which an excess of magnesium chloride has been added. This profound deviation from normal development, evoked by so slight a change in the environment, emphasizes the delicate precision of the processes through which normal minnows develop in their normal aquatic environment.

Charles Darwin's interest in genetics was a consequence of his studies of evolution. It will be necessary, therefore, to give a brief statement of his evolution theory in order to show its relation to genetics.

Darwin imagined that evolution occurred in this manner: Among the individuals of any species there would be many differences. For example, some might be slightly larger than the average, or have longer legs, or have a thicker coat of fur. If any of these variations made their possessors better adapted to survive, those with the better characteristics would have a greater chance of leaving offspring—survival of the fittest. With the passage of time the original population would change, its individuals gradually becoming larger, or developing longer legs or a thicker coat of fur, or whatever characteristic was of value for survival. In this way one species could evolve into another or give rise to two or more different species. For the present we should merely note the importance of variations. Therefore, Darwin in 1868 realized that his theory must be based on a sound understanding of the mechanism of inheritance.

To develop a knowledge of heredity we must have variations. A species showing striking differences between individuals becomes for this reason valuable to us from the standpoint of genetics. If every person, for example, had brown eyes, we should know nothing as to the nature of the inheritance of eye color in man. But, when in the midst of a brown-eyed population we meet a blue-eyed person, we begin to collect data on heredity of the color of eyes. Variations, especially striking variations, then, make a convenient introduction to genetics.

PART I MONOHYBRID

Scattered throughout previous bulletins are articles touching on genetics and using varied descriptive terms and processes. It is the intent of the author to explain and use universal genetic references that are modern and scientifically accepted. The key to maintaining and improving good strains of guppies or any other form is genetics. And any discussion of genetics would be incomplete without a word about the father of that branch of science, Gregor Mendel (1822). Not only was he the first to apply mathematics in examining biology, but he isolated his work from any outside influences, he used an exacting scientific approach working with thirty-two different types of the garden pea plant, he tested for pure strains and found some with yellow or green seeds, smooth or wrinkled seeds, red or white flowers, inflated or constricted pod form, green or yellow pod color, and tall or dwarf stem length. Using these various different pure strain **TRAITS** he crossed them and found for example that **ALL** the flowers from plants produced by a cross of red flower plants and white flower plants were **RED F-1**—no white or pink or any other color. These resultant traits and all such expressed traits Mendel called **DOMINANT**. What happened to the white flower trait—was it destroyed or lost? No it was not there but not expressed. It could not be seen, Mendel therefore, called such traits **RECESSIVE**. When a female of the **F-1** generation was pollinated with a brother of that same **F-1** generation it produced an **F-2** generation. The traits that disappeared in the **F-1** generation reappeared in the **F-2** generation. If you analyze the results in the following table, as Mendel did, you will notice that the dominant and recessive traits appear in the **F-2** generation in ratios of about 3:1.

F ₁ Original Crosses			F ₂ Generation		
Trait	Dominant	x Recessive	Dominant	Recessive	Total
Seed form	Round (R)	x Wrinkled (r)	6,474	1,850	7,324
Seed color	Yellow (Y)	x Green (y)	6,022	2,001	8,023
Flower color	Red (W)	x White (w)	705	207	912
Pod form	Inflated (I)	x Constricted (i)	882	299	1,181
Pod color	Green	x Yellow	428	152	580
Stem length	Tall	x Dwarf	787	277	1,064

How do these recessive traits disappear so completely and then reappear again, and always in such constant proportions? Mendel's greatest contribution was his answer that the constant proportions could only be explained if hereditary characteristics are determined by discrete (**separable**) genes. These genes Mendel saw must occur in the offspring as **pairs**, from factors inherited from each parent. These gene pairs separate again when the mature offspring produces its own sex cells, resulting in two kinds of gametes (**sex cells**), with one gene of the pair in each. Before separating each pair can have one more dominant gene (**W**) and one more recessive gene (**w**) (**Ww**), or two more dominant (**WW**) or two more recessive (**ww**) genes...same for the female. This hypothesis is known as Mendel's first law, or the **PRINCIPLE OF SEGREGATION**.

The two genes in a pair might be the same and in a self-pollinating plant would breed **TRUE**. When the genes of a gene pair are identical (**WW**) or (**ww**), the plant or animal is said to be **HOMOZYGOUS** for that particular trait. An individual that is Homozygous for any particular trait is known as **PUREBRED** and will breed true when crossed with each other. On the other hand, if the gene pair is different (**Ww**) they

are known as **ALLELES** (Two genes forming a contrasting pair, the adjective formed from this word is allelic. members of a pair or series of different hereditary factors that may occupy a given locus on a specific chromosome and that segregate in formation of gametes) and are said to be **HETEROZYGOUS** for that trait, (a **Metro- pair**). An individual that is Heterozygous for any particular trait is called a **HYBRID** refers to the offspring of parents which are each genetically pure (homozygous) for one or more pairs of hereditary factors, but with the two parents being homozygous for different members of allelic pairs or series. In practice the term has been extended to include offspring of species crosses, to progeny of crosses of inbred lines, and in some cases to breed crosses, and it will not breed true for that particular trait.

One gene may be dominant over another gene and the offspring would appear as if it had only one type of gene, this outward appearance is known as it's **PHENOTYPE**. However, in its genetic makeup called **GENOTYPE**, each gene (dominant W and recessive w) still exists as independent discrete units that will separate again when gametes (sex cells) are formed.

DISCUSSION:

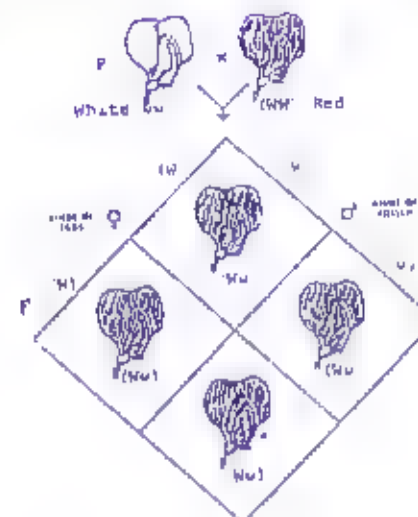
A pea plant homozygous for red flowers is represented as (WW) in genetic shorthand. The capital (W) indicates it is dominant, the lowercase (w) indicates it is recessive. A (WW) plant can produce male or female sex cells but each will carry the same red flower producing (W) gene (one half of a WW genotype). A white pea plant (ww) can produce sex cells with only a white flower producing (w) gene. When a (w) male cell fertilizes a (W) egg cell, the result is a F₁ (Ww) pea plant, which since the (W) gene is dominant, can only produce red flowers. This F₁ generation plant can produce egg or sperm sex cells (gametes) with either a (W) or (w) gene. And if it self pollinates, four possible crosses can occur: (Ww) x (Ww).

- Male (W) x female (W) — red flowering plant (WW)
- Male (W) x female (w) — red flowering plant (Ww)
- Male (w) x female (W) — red flowering plant (Ww)
- Male (w) x female (w) — white flowering plant (ww)

How can we diagram this procedure into a simple working example? A square or checker board type arrangement will suffice for just a few or many complex independent gene combinations. A **PUNNETT square**, as it is called, is made by listing the hereditary genes that could be present in each parent's gamete. As you can see below the male gametes (sperm or pollen) are listed along one edge of the square, and the female gametes (egg) are listed along the other edge. The boxes are then filled in with all the gamete combinations that could occur in the offspring. The use of a **PUNNETT square** for the determination of possible genotypes (genetic makeup) is done on p53 for the cross pollination of a red (WW) plant with a white (ww) plant which resulted in all offspring plants (Ww) producing only red flowers, because of the dominant (W) of the genotype in 100% of the offspring.

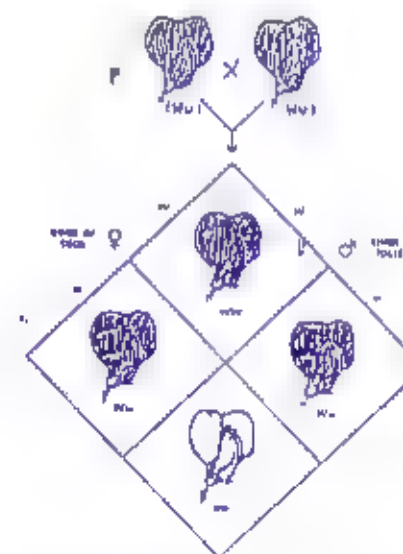
Note that we are dealing with only independent dominant and independent, recessive traits: they do not merge, dilute or change the trait as in this example the color. It can only be either red or white: it can not form a plant that will produce a pink flower or a red flower with a white border: those type changes will be covered in later articles.

Figure #1



Another square is used for the determination of possible genotypes produced by inbreeding the F₁ generation with itself (brother x sister) Ww x Ww who both produced only red flowers.

Figure #2



Note the ratio phenotype (outward appearance) of 3 red flowering plants to 1 white flowering plant. Within this same 3:1 phenotype ratio, however, note the genotype ratio of 2:1.

- 25% One part Homozygous red — (WW) (pure strain will breed 100% true)
- 50% Two parts Heterozygous red — (Ww) (Hybrid with recessive gene)
- 25% One part Homozygous white — (ww) (pure strain will breed 100% true)

TESTING THE HYPOTHESIS: THE TESTCROSS

In devising a test for his hypothesis, Mendel established a pattern of testing that has been used often ever since. It is called a **TESTCROSS**, and is performed by mating two individuals. One of these is a known **homozygous recessive** genotype (such as (ww)), the other's genotype for color is unknown. It may be either **heterozygous** such as (Ww) or **homozygous** (WW) but it is not apparent from the physical characteristics of the phenotype (example it is a red flowering plant). In the example found in figure #3 the cross would be (Ww) x (ww). Can you now predict the ratio between the white and red flowering plants resulting from such a cross?

	w	w	
W	Ww	Ww	50% Heterozygous
w	ww	ww	

Figure #3

	w	w	
W	Ww	Ww	100% Heterozygous
W	Ww	Ww	

Figure 4

All possibilities are equal according to the Punnett Square. Therefore, half of the plants resulting from such a cross are expected to have a genotype of (Ww), and would produce red flowers. The other half of the plants are expected to have a genotype of (ww), and would produce white flowers. Thus, crossing a heterozygous with a homozygous recessive individual produces **BOTH** a genotype and a phenotype **RATIO** of 1:1. —50%

If on the other hand, however, suppose the unknown had been homozygous dominant (WW)? Using a Punnett square again we would find all genotypes produced by such a cross to be (Ww) and would all produce red flowers. —100% (figure #4)

Lets clarify the importance of using a homozygous (ww) recessive in the testcross. If you tried to use the dominant (WW) genotype with any unknown, either (Ww) or (ww) or (WW), the results produced would be the same phenotype — red flower producing plants in all cases. There would be no differences in the resulting percentages because the dominant gene (WW) masked your test sample. on the other hand the recessive gene allows a 50% or a 100% test result indicating the exact genotype used in the test sample.

APPLICATION:

For the sake of simplicity, let us take a beautifully colored full finned male guppy (gray line strain) with exceptional vigor that took "Best of Show" and you were able to purchase. Along with a giant well proportioned gold female guppy that you bought at the same time. When you arrive home, you find your teenage son has a fish sale and all your tanks are empty, but he hands you a can full of money! What do you do about developing a new fish line? Well, you breed what you have which appears to be two beautiful

specimens. The gray male is dominant (GG) and the gold female is recessive (gg). As shown in figure #1 the offspring from such a cross would be (Gg) genotype and have a gray body phenotype. No outstanding characteristics are evident in these hybrid young, so you mate the offspring, brother x sister (Gg) x (Gg). This cross would produce the same results obtained in Punnett square figure #2. A ratio of 3 gray bodied guppies to 1 gold bodied guppy (**PHENOTYPE** ratio 3:1), and a ratio of 1 part Homozygous (GG), gray guppies, 2 parts Heterozygous (Gg) gray hybrid guppies, and 1 part Homozygous (gg) gold guppies (**GENOTYPE** ratio 1:2:1).

Let us say for example that the male gold guppies (gg) are developing a terrible caudal. You want to destroy the gold strain but get the gray strain as pure as you can because you have a few excellent young gray males with all the characteristics you hoped for. **WHAT DO YOU DO NOW? HOW?** First you count the offspring and find 32 (for the sake of keeping it simple) and that 25 of them have the phenotype desirable traits you want. Again say we have half the drop divided evenly between males and females. Therefore, if 1/4 of the male drop were just what you want (GG), 1/4 should be gold (gg) and discarded, and 1/2 are hybrids (Gg) exhibiting, in this case, no beneficial phenotype qualities. You may want to destroy the hybrids or you might be willing to work with them in crosses to obtain 25% of their drops with the desired traits.

Now for the females, the only method of truly determining which are homozygous (GG) is to **TESTCROSS** them with their gold brother or any gold male (gg) and if they throw a 50% ratio of 1 gray 1 gold, then the female was **HETEROZYGOUS** and all her gray offspring F-3 would be heterozygous and should be destroyed. Only if the offspring were to be all 100% gray phenotype could we be sure she was homozygous (GG). Remember that randomly breeding sister and brother (Gg) x (Gg) will give 50% genotype (Gg) that are gray phenotype but hybrid and will develop poor caudals (in this particular strain). With a breeding of (Gg) x (Gg) you will still get 50% of the offspring with (Gg) genotype along with 25% gold guppies. How many generations will it take you to breed out the (Gg) genotype? With random breeding (not knowing which genotype you are using), probably never. With a testcross you know which are the female (GG) homozygous genotypes that will continue to give you a pure strain and breed true.

PART II DIHYBRID

MENDEL AND THE LAWS OF CHANCE:

In applying statistics to the study of genetics, the laws of chance apply to biology as they do to the physical sciences. Toss a coin. The chance that it will turn up heads is fifty-fifty, or 1/2. The chance that it will turn up tails is also fifty-fifty, or 1/2. The chance that it will turn up one or the other is certain, or one chance in one. Now toss two coins. The chance that one will turn up heads is again 1/2. The chance that the second will turn up heads is also 1/2. The chance that both will turn up heads is 1/2 x 1/2, or 1/4.

The probability of two independent events occurring together is simply the probability of one occurring alone multiplied by the probability of the other occurring alone. The chance of both turning up tails is similarly 1/2 x 1/2. The chance of the first turning up tails and the second turning up heads is 1/2 x 1/2, and the chance of the second turning up tails and the first heads is 1/2 x 1/2. We can diagram this in a Punnett square:

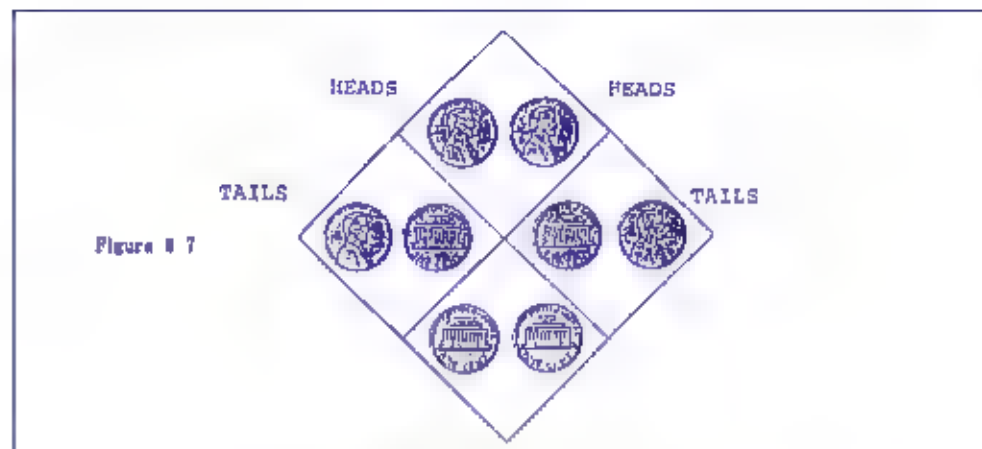


Figure # 7

Notice: That the chance of both coins coming up heads is 25%
 That the chance of both coins coming up heads & tails is 50%
 That the chance of both coins coming up tails is 25%
 100%

If heads would indicate a dominant gene we would have a phenotype ratio and a 1:2:1 genotype ratio. So you see there is no big mystery if we look at genes following the laws of probability and chance....or is there?

Up to this time we have confined our study to single pairs of traits: red vs. white flower, round vs. wrinkled seeds, yellow vs. green seeds. Is there a relation between the different pairs? Mendel produced plants that bred true for two traits. Some plants would produce round yellow seeds through successive inbred generations, for example, and others would produce wrinkled-green seeds. Since the genes in each pair were identical for each trait, the genotype (genetic make up) for round-yellow seeds is (RRYY) and for the wrinkled-green seeds (rryy). Both are homozygous (capital letters denote dominant, lower case denote recessive characteristics). When crossing both of these seeds the genotype for each breaks up into as many paired combinations as is possible, in this case (RRYY) - all (RY)s and (rryy) - all (ry)s as shown in the Punnett square below.

All F₁ offspring were round and yellow phenotype and (RrYy) genotype (dominant R round, dominant Y - yellow)

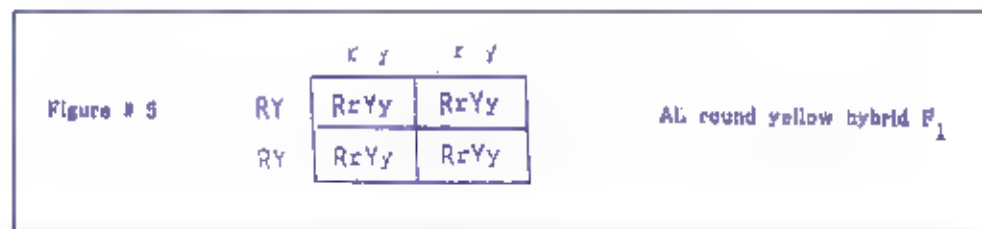


Figure # 8

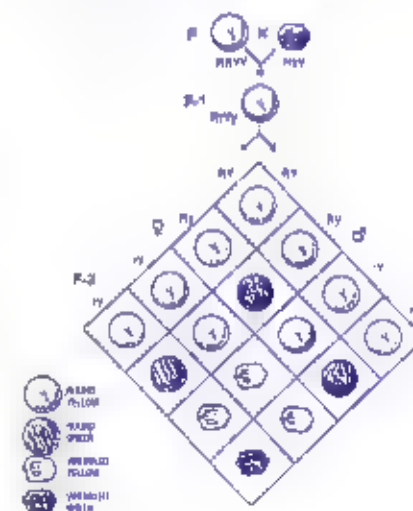
All round yellow hybrid F₁

Now is when this starts to get interesting, let us breed the F₁ offspring (RrYy) genotype with itself. We obtain the two original homozygous types we began with: round-yellow (RRYY) and wrinkled-green (rryy) but in a 9:3:3:1 ratio. We also derive two new phenotype seeds we did not have when we started. We developed round-green seeds (RrYY genotype) and wrinkled-yellow seeds (rrYy genotype). The overall ratio is 9:3:3:1.

		RrYy			
		RY	Ry	rY	ry
RrYy	RY	RRYY round yellow	RRYy round yellow	RrYY round yellow	RrYy round yellow
	Ry	RRYy round yellow	RRyy round green	RrYy round yellow	Rryy round green
	rY	RrYY round yellow	RrYy round yellow	rrYY wrinkled yellow	rrYy wrinkled yellow
	ry	RrYy round yellow	Rryy round green	rrYy wrinkled yellow	rryy wrinkled green

Figure # 9

Does Mendel's earlier law still apply? Do the round and wrinkled seeds still appear in the 3:1 ratio (dominant to recessive phenotype), as well as the "yellow to green seed ratio? Count them and see if you don't find 12 round seeds and 4 wrinkled seeds or a 3:1 ratio. Also we still have 12 yellow seeds to 4 green seeds or a dominant to recessive ratio of 3:1. New combinations of traits were created from the dihybrid cross because the alleles (each member of a pair or combination of genes) for seed shape and color were separated, assorted and distributed independently of each other during the production of gametes. The concept that pairs of alleles can be assorted independently of each other is known as Mendel's second law, the PRINCIPLE OF INDEPENDENT ASSORTMENT.



DISCUSSION Now can we start to make use of these findings and the laws of genetics? Suppose we find a strain of male guppy with a small fin fish, red dorsal. Red is usually a dominant color and is very often a problem to remove in other strains because it is so dominant. Now if we look for a strain which

consistently produces large fish dorsals with little or no color and cross them, we can plan on producing a new type male with a large brilliant red dorsal! You really think so. How confident are you with what was covered so far?

Yes, it is possible but "WHEN" you ask? If the red is dominant (R), and we can be fairly sure that it is, and if the large size dorsal gene is dominant (Y) then let (y) indicate the small dorsal and (r) indicate the clear or light dorsal color. In this case we will have our desired result in the first generation F₁. Again RRyy — brilliant red, small dorsal; and (rrYY) clear or light, large dorsal. Then RRyy x rrYY all RrYy, figure # 5, in which the phenotype would be brilliant red large dorsal, male F₁. However when we breed this generation we will not have a pure strain, what we are looking for is RRYy or we can continue the RRyy strain along with the rrYY strain and continue to cross them to obtain the desired brilliant red large dorsal males and throw away all the females F₁.

On the other hand, if the small size dorsal gene is dominant (Y), and the large dorsal gene is recessive then according to figure # 4 all male dorsals will be brilliant red and small in the F₁ generation (RrYy genotype). Raising this generation and breeding the F₁ x F₁ (brother x sister) as in figure # 5, we will have a male ratio of 9 red small dorsals (RRYY) 3 red large dorsals (Rryy) 3 clear small dorsals (rrYY) 1 clear large dorsal (rryy).

Let's keep things simple and say we have a drop of 32 of which 16 are male and 16 female. Of the 16 males we should have three red large dorsal fish to choose from because the phenotype shows the genotype, but only in the male. Now we come to the 16 females, only three of which carry the (Rryy) genotype to give us a pure strain. We can breed the selected male to all 16 females, separate the drops in sixteen tanks and then divide the sexes and tie up 32 tanks. When you can see the dorsal color you can discard those four drops that have clear dorsals (rrYy & rryy) and free eight more tanks, then mate the remaining red dorsal fish until the size difference is very apparent and discard 18 more tanks (RRYY). You now have a strain in the remaining 8 tanks (Rryy) that will throw 75% pure brilliant red large dorsals as shown in figure # 7.

		Rryy	
		RY	ry
Rryy	RY	RRYY	Rryy
	ry	Rryy	rryy

Figure 7

Note that 25% of this drop will be RRYy and by using a testcross with all recessive genes (rryy) you can finally select the females (Rryy) that will produce a strain that will breed 100% true for large red dorsals.

Homozygous RRYy x homozygous rryy will give 100% heterozygous F₁ offspring, whereas heterozygous Rryy x homozygous rryy will give a 1:1 ratio of 50% heterozygous Rryy and 50% homozygous rryy in F₁ offspring.

There is a saying that one may miss seeing a forest because of the trees. For those who study genetics a parallel proverb might be devised to say that "one may fail to understand genetics because of the genes". Let us see what is meant by this paradoxical statement.

Most of us would concede that a forest is made up, at least in large part, of trees, and that trees largely determine the character of a forest. To understand a forest, then, we must examine the trees. But as we stand close, to a tree to scrutinize it carefully, it appears as a huge bulk, and may cut off our view of other trees and other objects in the forest. Especially, it may obscure various cross relationships among the components of the forest. For comprehension of a complex whole made up of many parts, it is necessary to look **NEAR, FAR, AND ALL ABOUT**.

Similarly, all present evidence leads us to conclude that genes have great importance in determining the character of an organism. If we are to get at an understanding of heredity and life, we must analyze the nature and behavior of genes. But if genes are to be studied effectively, they must be dealt with only a few at a time. Otherwise the problems of the geneticist become too complex to analyze. This difficulty begins to become apparent even in the relatively simple analyses dealing with segregations of Mendelian trihybrids. And remember that to deal with the segregation of genes is to consider only a single aspect of their behavior.

Actually in calling an organism a Mendelian trihybrid, and in using similar terms and concepts, we create an artificial kind of situation. Real genes are never found in the situation we give them when one or two genes are set apart, designated by letters or other arbitrary symbols and shown in splendid isolation on a printed page. Geneticists estimate that the different kinds of genes in most organisms number in the hundreds or even the thousands. As a given gene functions in an organism, it has a chemical environment determined not only by itself but also by many other genes and by agents of the external environment of the organism. More or less specifically, and to a greater or less degree, the functioning of a gene always depends on this environment.

Genes are generally recognized by the characteristics primarily determined by them. They are so named after the characteristics they determine. These are expedient procedures and well justified. But you must remain aware that genes and characteristics are not identical. The expression of a given characteristic, even though it is primarily associated with a single gene, is the product of many interactions between genotype and environment. If you fail to understand this, one of the major concepts of genetics will have escaped you. **GENES DETERMINE POTENTIALITIES** — the realization of these potentialities depends on the environment in which the genes perform their functions. Genes do not exist within an environmental vacuum, neither do they function entirely without reference to their fellow genes. The activities of genes may be influenced by the internal environment of the organism or by factors of the external environment. The same genotype may give rise to different phenotypes under varying circumstances of environment. In turn, one environmental factor may set to elicit various responses, depending on the genotype of the organism. In some instances, it is helpful to think of genotypes as determining thresholds for response.

Apparently inconsequential differences in environment may assume special importance at critical times in the development of an organism. This principle can be seen in characteristics of a giant race of *Drosophila*, where a single genotype may produce individuals falling into two distinct categories, normal-sized flies and giants that average 70 percent greater in weight than do wild-type adults. In a culture of *Drosophila* of this genotype, frequency of giants depends rather directly on the cultural conditions as expressed in food available for each larva. When conditions are crowded, and when there is rigorous larval competition for food, few giants emerge. With plentiful food available for each individual potential, giants actually become giants in high percentage. Wild-type *Drosophila* do not become giants even under the most favorable nutritional circumstances that have been devised.

It is interesting that in homozygous giant cultures grown under conditions where nutrition may be a limiting factor, it is not so much the size of the giants but their number that is affected. The few giants that do appear are about as large as those emerging in culture bottles where nutritional conditions are uniformly excellent. This suggests that there is some kind of **genetically controlled THRESHOLD** for the reaction that produces the giant characteristic. The reaction itself seems to be set in train by factors of the environment, in this instance probably nutritional factors. Under the somewhat variable conditions of a crowded Drosophila culture, these factors may reach threshold intensity for some individuals but not for others. The threshold concept is a useful way of looking at a number of the relationships between heredity and environment that will come to your attention. You should realize, however, that it provides only a point of view and is not in itself an explanation of particular cases where a genotype shows irregular expression.

Up to this point we have been considering various aspects of interactions of genes and environment with reference to the realization of genetic characters. These interactions are supposed, although they cannot always be specifically proved to operate through chemical reactions originated by the genes. In the ordinary interplay of genotype and environment, the genes themselves are not altered, at least not permanently. Sometimes, however, a gene does undergo sudden, permanent, apparently spontaneous alteration into a different allelic form (mutation). The conditions responsible for the processes by which spontaneous mutation occurs have not been identified, but treatment with certain drastic environment agents, like X-rays, ultraviolet light, or mustard gas, greatly accelerates the mutation frequency of genes. These agents do not appear to act selectively in the sense of reacting only with particular genes, but rather they seem to increase mutation rates in general. In addition, there is evidence that a few particular genes may be able to induce, or at least facilitate, the mutation of other genes. This is not unexpected, since genes play a large role in determining the internal chemical environment of the organism.

Part III

Genes and the Chromosome Theory:

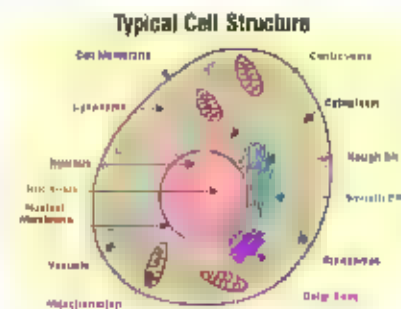
As the body cells were investigated in the early part of this century, no separate genes could be found, but from the action of chromosomes in cell division it was surmised that they must be located on these structures. The common fruit fly was used in experiments because of the advantages it offered. It is very small, requires no special care or food, one sex hatches earlier than the other so separation is easy, and certain cells in the salivary glands have chromosomes almost 200 times larger than the chromosomes in other cells. This large size made easy observation of the physical structure, on which gene location could be identified.

When Mendel's conclusions were rediscovered and announced to the world, it was soon noted that a striking series of parallels existed between the behavior of genes on the one hand and the behavior of chromosomes on the other hand. Let us look into the behavior of chromosomes and see how it parallels the behavior of the genes. We shall thus come to some conclusions as to what genes are.

First of all, we can readily see by microscopic examination that living organisms are composed of minute structural units. These we call cells. And parts of the organism seem to be made up of these cells, more

or less regularly arranged. When we examine them we find that, while they apparently differ considerably in shape and appearance, practically all seem to possess one characteristic in common, a more or less spherical nucleus somewhere in the interior of the cell.

The material of which cells are composed is known as protoplasm. It is the living material of our world. Part of the protoplasm forms the nucleus of each cell. The rest of the protoplasm, different in appearance and structure, is known as cytoplasm. We find this to be the basis of the differences in general appearance of cells. The nuclei of all the cells of an organism are surprisingly alike. It is to the nucleus that we must turn our attention for the analysis of the physical basis of heredity.



All the millions of cells in our bodies have come there by division and subsequent growth from other cells, originally tracing back to the single fertilized egg cell from which each individual arises. Every cell if we could watch it long enough, would be seen either to die or to divide. The knowledge of what happens when a cell divides is of fundamental importance in understanding heredity.

MEIOSIS VS MITOSIS.

The events that take place during meiosis somewhat resemble those that take place during mitosis, and meiosis, which is believed to have evolved from mitosis, uses much of the same cellular machinery. But there are a number of differences between them, of which three are of salient importance.

First, and most obvious, meiosis takes place in two stages involving two successive divisions and resulting in four new nuclei instead of two.

Second, whereas mitosis produces two nuclei that are identical to each other and to the parent nucleus from which they are formed, meiosis results in four nuclei that are not necessarily identical to each other and that have only half the number of chromosomes present in the parent nucleus.

Third, near the beginning of meiosis (but not mitosis), the chromosomes arrange themselves in homologous pairs, that is, each chromosome pairs up with another chromosome of the same size and shape, its homologue.

MITOSIS When a cell is not dividing, we speak of it as being in the interphase. When we look within the nucleus we see what appears to be an irregular network of chromatin material (named so because it is usually colored or stained by certain dyes). This network is interpreted as a series of long coiled threads of chromatin. When the cell is about to start its process of division, we find that the coiled threads become more definitely noticeable. Now we can see that each thread



is really double, having duplicated itself throughout its entire length. The two halves are identical in appearance and remain so closely applied to each other that they appear as one, except under very high magnification. The two halves are imbedded in a translucent matrix.



The threads now shorten and thicken, each forming a tight spiral coil. They thus appear as rod-like, sausage-shaped, or V-shaped bodies. These bodies are called chromosomes. By this time the nuclear membrane has dissolved away and it is possible to count the number of chromosomes since they are now much more definitely separated one from the other. There are two important and interesting facts. First, with few exceptions, the chromosomes occur in pairs; that is, for each chromosome which we identify there is another one similar in appearance. Second, the number of chromosomes is in general constant for any given species.

While the threads have been forming into spiralled rods (chromosomes), fine fibers have been radiating from opposite ends of the cell toward each other. In animal cells these fibers radiate from small bodies known as centrosomes. The centrosome at each end of the cell, got there by migration from the centrosome which at the interphase was at one side of the nucleus. As the chromosomes were forming, & dividing, the two halves moved to opposite sides of the nucleus, and from them the fibers radiated. The stages of cell division up to this point constitute the **PROPHASE**.



The spiralled fibers become attached to the chromosomes which have by now become arranged in a flat circle across the interior of the cell. This stage is known as the **METAPHASE**. Each chromosome (which is really double because it has already split longitudinally) now separates into its two halves. The two halves of each chromosome now pass to opposite poles of the spindle, apparently pulled by certain of the spindle fibers. Half of each chromosome goes to one end of the cell, half to the other. We can see that the division is quantitatively equal and we shall show later it is also qualitatively equal. We call this stage the **ANAPHASE**.



The "daughter chromosomes" at each end of the cell then lengthen out again into long threads, and a nuclear membrane forms around each new group of chromosomes. The cytoplasm divides, forming two new cells, within each of which is one of the new nuclei. This constitutes the **TELOPHASE**. The division of the cytoplasm, however, is not necessarily equal, as in the division of the nucleus. The new cell, each approximately half size of the cell from which they were formed, will grow to full size before they in turn divide.

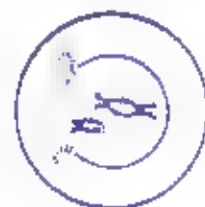


This whole process of division is known as **mitosis**.

THE MATURATION OF THE GERM CELLS Reproductive division of a cell occurs in formation of the germ cells, or gametes. The entire process of the formation of the gametes is known as **maturation**.

Potential sex cells divide frequently by mitosis; every so often groups of these cells undergo a series of events leading to the formation of mature sperm or eggs. Let's follow one event through such a transformation.

After enlargement of the sex cells, called **spermatogonia**, it is called a primary spermatocyte. A brief resting period and then the chromosomes appear as slender coiled threads, as in the prophase of mitosis. This time, however, the two chromosomes of each pair become closely applied to each other throughout their lengths. This is known as **synapsis**. While they are thus intimately associated, each chromosome splits, so that there are now four strands, **chromatids**, in close association. The two chromatids of a chromosome are spoken of as a **dyad**; the two dyads (four chromatids) in close association as a **tetrad**. Following synapsis the four chromatids of the tetrad tend to loop out in pairs in a twisted formation.



The spindle fibers attach to one dyad of each tetrad, the two dyads of each tetrad then separate and pass to opposite ends of the cell. The two new cells thus formed have only half the number of chromosomes found in all other cells of the species. These new cells with half the number of chromosomes are called **secondary spermatocytes**.

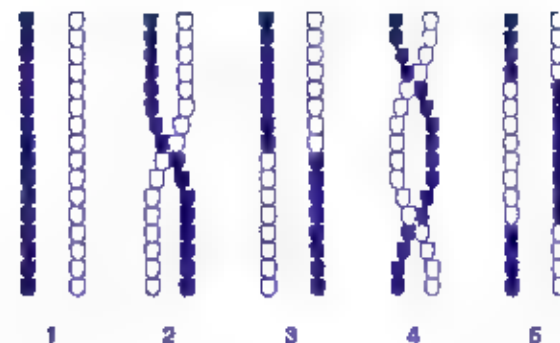


The secondary spermatocytes then divide, each chromosome separating along the split that occurred during the formation of the tetrad described above. These newly formed cells are called **spermatids**. There will be four spermatids from each original spermatogonium which underwent the maturation process. The spermatids then transform into sperm without any further division, usually by condensing and developing a tail piece from the cytoplasm leaving the head of the sperm composed almost entirely of the nucleus which contains the chromosomes.



One important event, which takes place during the reduction division and must be emphasized because it has an important bearing on heredity, is this: When the two members of a pair of chromosomes are closely apposed in synapsis, while they are still long drawn out and before the actual reduction division, each becomes, as was pointed out, split longitudinally, although the two halves of each chromosome remain close together. There are thus four threads closely associated in each pair of chromosomes (the tetrad).

When the two members of a pair of chromosomes separate after synapsis, it is seen that they separate in a peculiar crossed manner. Each cross is called a **chiasma**. It is interpreted to be the result of the exchange of segments between two of the threads belonging to different members of the pair. We have seen that the two chromosomes of a pair may exchange material with each other before separating, and two of the four sperms from a primary spermatocyte may each contain a chromosome which is not identical with the corresponding chromosome in each of the other two sperms.



Diagrammatic representation of single crossing over between homologous chromosomes 1-3; and double crossing over 4 and 5.

In the formation of mature ova, or eggs, from potential egg cells in the ovary, a similar series of events takes place. The only difference is that instead of the process ending in four mature gametes, as it did in the case of males, three of the four resulting cells are small, and disintegrate. We speak of them as **polar bodies**. The fourth cell gets all the cytoplasm and becomes a mature ovum, larger than most cells of the body.

As a result of maturation, then, we have in males the production of sperms, each containing half the number of chromosomes which the body cells possess; and in females the production of egg cells likewise containing half the number of chromosomes which the other cells possess. This half number of chromosomes for any species we call the **HAPLOID**, or **N**, number of chromosomes. The number found in the other cells of the species we call the **DIPLOID**, or **2N**, number of chromosomes.

It is to be noted that the haploid number of chromosomes does not consist of any half of the diploid number, but always consists of one each of each pair of chromosomes. Chromosomes retain their individuality from generation to generation. In the prophase stage, when they do not appear as visible formid chromosomes, they are still entities. Under careful observation, through the microscope, the chromatin material of each chromosome is seen to be intact and independent of other chromosomes. Genes, too, retain their individuality. A pair of genes for dwarfness in the F-2 generation produces an individual just as dwarf as though in effect had not been hidden while being carried through the (all F-1) generation. Of course the exchange of material by homologous chromosomes is an exception to the statement that chromosomes keep their individuality, but later we shall find a comparable exception for groups of genes.

Thus we already have three paradoxes between the behavior of chromosomes and the behavior of genes. We saw a moment ago that either chromosome of a pair may occur in a gamete with either chromosome of any other pair, the only requisite being that there be one of each pair in every gamete, in other words, chromosomes assort at random.

In animals with a large number of chromosomes, an almost infinite number of possible combinations may be expected. In organisms with 23 pairs of chromosomes, for example, the probability that a gamete produced by an individual in the population will have any specific combination of chromosomes is $(1/2)$ to the 23rd power, which is in the order of one in eight million. This calculation is an underestimate due to the possibility of any crossing over, which is another source of variability. Further increased numbers of gene combinations are possible in zygotes that result from random fertilization. Much of the variation observed in natural populations can therefore be explained on the basis of the recombination of chromosomes and genes already present in the breeding population.

CROSSEOVERS:

Crossing over and independent assortment are the most important mechanisms for the generation of new combinations of genes. Natural selection then acts to preserve those combinations that produce organisms with maximum fitness, that is, maximum probability of perpetuation of the genotype. The important features of the concept of crossing over are summarized as follows:

1. The location of a gene on a chromosome is called a **locus** (plural, loci). The loci of the genes on a chromosome are arranged in a linear sequence. Sometimes the term locus is used to refer to the location of a set of contiguous genes with related functions.
2. The two alleles of a gene in a heterozygote occupy corresponding positions in the homologous chromosomes. That is, allele A occupies the same position in homolog 1 that allele a occupies in homolog 2.
3. Crossing over involves the breakage of each of two homologous chromosomes (actually chromatids) and the exchange of parts.
4. Crossing over occurs during the synapsis of the homologous chromosomes in prophase I (zygotene and pachytene) of meiosis. Since chromosome replication occurs during interphase, meiotic crossing over occurs in the postreplication tetrad stage, that is, after each chromosome has doubled such that four chromatids are present for each pair of homologous chromosomes. Crossing over that involves sister chromatids (the two chromatids of one homolog) occurs, but it is seldom detectable genetically since the sister chromatids are usually identical.
5. Chromosomes with recombinant combinations of linked genes are formed by the occurrence of crossing over in the region between the two loci.
6. The probability that crossing over will occur between the two loci increases with increasing distance between the two loci on the chromosome.

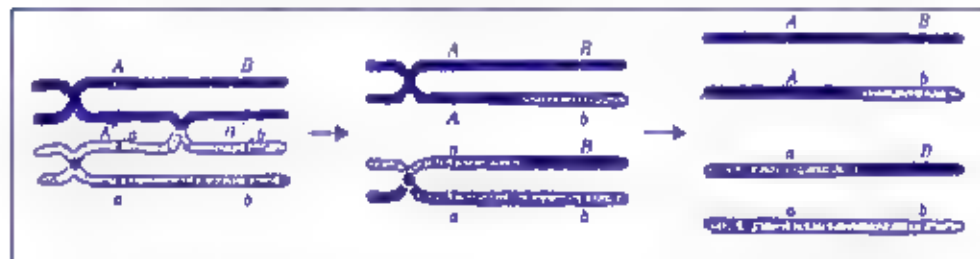


Diagram illustrating the occurrence of crossing over between two loci. Note that the crossover involves only two of the four chromatids of the pair of homologous chromosomes. These two chromatids interchange corresponding segments by a breakage and exchange mechanism. Also notice that of the four products of this meiotic event, only two contain recombinant combinations of the alleles of the two genes. The other two daughter chromosomes (top and bottom, right) carry parental combinations of the alleles of the genes.

SEX-LINKED GENES:

Work with the fruit fly (*Drosophila*) usually showed normal red-eyed individuals. When a white-eyed male turned up it was crossed with red-eyed females, giving 1,240 offspring all with red eyes except three. Now if the red-eye phenotype is dominant and if the gene causing it is distributed in accordance with Mendel's laws, you would expect all the F₁ generation to have red eyes. The red-eyed males and females of the F₁ generation were crossed and an approximate 3:1 ratio red-eyed to white-eyed flies was obtained. This is roughly within the range of what you would expect except for one thing, there were no white-eyed females; all white-eyed flies were male. This seemed to contradict Mendel's principle of independent assortment. Upon examination there are four pairs of chromosomes in the cells of the fruit fly, in the female all four pairs contain homologous chromosomes. However, in the male, only three pairs have homologous chromosomes. In the fourth pair, the chromosomes are dissimilar. One, called the X chromosome, resembles one chromosome in one of the pairs in the female. The other, called the "Y" chromosome, has a hook on one end and is only found in the male. The X & Y chromosomes are referred to as **sex chromosomes** because they are associated with the sex of the individual. All other chromosomes are called **autosomes** (non sex-related).



Male gametes (sperm cell) contain either an X or Y chromosome. Female gametes contain only X chromosomes, never a Y. A normal zygote (fertilized cell) resulting from fusion of a male and a female gamete has either two X chromosomes and becomes a female or it has an X & Y and becomes a male. Investigations of sex determination have shown that the embryo is bi-potential, having the ability to develop into either sex. Determination for one sex or the other is usually accomplished by a balance between genetic factors for maleness and those for femaleness. Several different combinations involving chromosomes, genes, cytoplasm, and hormones have been associated with this balance, particularly in the secondary sex characteristics. Hormones influence the expressions of some genes. Sex chromatin bodies that result from the inactivation of one X chromosome in normal female are useful for determining the genetic sex of abnormal fetuses and intersex individuals. Cells of normal males have no sex chromatin bodies. The number of sex chromatin bodies in individuals with more than two X chromosomes is one less than the number of X chromosomes. Genes other than sex determiners are also located on sex chromosomes. They behave according to the segregation pattern of these chromosomes and are **sex-linked**. Morgan discovered sex-linked inheritance in *Drosophila* which led him to assume that the female *Drosophila* possessed two X chromosomes which were both sex determiners and the carriers of sex-linked genes, and that the male possessed only one x-chromosome. Later it was discovered that the male *Drosophila* possessed a mate to the X-chromosome, that was distinguishable from the X because it commonly had a hook on one end. This chromosome was called the Y-chromosome.

It was found that the gene for eye color is located only on the X chromosome and there is no allele for eye color on the Y chromosome. The gene for red eye color is dominant. Dominance is applied to one member of an allelic gene pair that has the ability to manifest and show its trait at the exclusion of the expression of the other allele of the gene pair. The gene for white eye is recessive. Recessive is applied to

one member of an allelic gene pair that lacks the ability to manifest or show its trait when the other or dominant member is present. If we let X & Y represent the sex chromosomes, R the allele for red eyes, and r the allele for white eyes we can symbolize the cross as follows:

$$\begin{array}{ccc} X^r Y & \times & X^R X^R \\ \text{(white eye male)} & & \text{(red eye female)} \end{array}$$

Figure 1-9

Note the recessive allele is the only one in the male, since there is no comparable allele on the Y chromosome. Therefore, this recessive gene expresses itself as though it were a dominant gene. We get the following results in the F₁ generation:

	X ^R	X ^R	
X ^r	X ^R X ^r	X ^R X ^r	
Y	X ^R Y	X ^R Y	F ₁ = 2X ^R X ^r : 2X ^R Y

Thus, two genotypes can occur in the F₁ generation: X^RX^r and X^RY. There are also two phenotypes, red-eyed female and red-eyed male.

In a cross between a female and a male of the F₁ generation:

$$\begin{array}{ccc} \text{Red-eyed female} & & \text{Red-eyed male} \\ X^R X^r & \times & X^R Y \end{array}$$

Four possible genotypes and three possible phenotypes can result.

Egg		Sperm	
X ^R	x	X ^R	= X ^R X ^R (red-eyed female)
X ^r	x	X ^R	= X ^R X ^r (red-eyed female)
X ^R	x	Y	= X ^R Y (red-eyed male)
X ^r	x	Y	= X ^r Y (white-eyed male)

	X ^R	X ^r
X ^R	X ^R X ^R	X ^R X ^r
Y	X ^R Y	X ^r Y

$$F_2 = 1 X^R X^R : 1 X^R X^r : 1 X^R Y : 1 X^r Y$$

Note that there is a 3:1 ratio between the red-eyed and white-eyed phenotypes. There are no white-eyed females in the F₂ generation. They can be produced in the F₃ generation with a white-eyed male (X^rY) and a heterozygous red-eyed female (X^RX^r) cross. Can you Work out a Punnett square for such a cross?

Any gene located on the sex determining chromosomes are called **SEX LINKED** genes or **X LINKED GENES**. The chromosome is in effect a string of many different alleles—any of the different possible forms of a single gene. Alleles on a single chromosome tend to remain linked and are called **LINKAGE GROUPS**.

The traits in Mendel's peas assorted independently, which implies that their alleles were unlinked and on separate chromosomes.

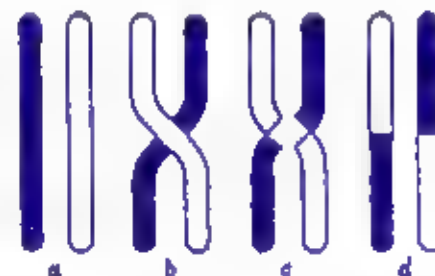
Had the genes in the pea plants been linked, Mendel would not have been able to produce the clear cut results he attained with his **VERY LUCKY** selection of the pea plant and with his limited study of genes (or what he called factors) which in these cases were independently assorted. **LUCK** has played a big part in many of the great discoveries of our times.

Therefore, we might expect that alleles on different chromosomes would always remain unlinked, and those on the same chromosome would always remain linked. But this is not always true. During meiosis (the process of cell division that results in the formation of a gamete containing a single set of chromosomes) the paired chromosomes line up alongside each other before they divide. At this time the ends or any parts of the inner two chromosomes (a pair of duplicated chromosomes, but have not yet separated from each other) may break off and be exchanged between the two chromosomes and this is called a **CROSSOVER**.

Genes producing the characteristics you are working towards with your fish if located on the sex chromosomes, can lead to some frustrating moments. It is not unlikely that at times genes on autosomes can cross over and become incorporated in a sex chromosome. Some breeders are convinced that the X chromosome causes some of the gene traits they desire, such as bright colored and large caudal size in the female. Since the female never has a Y chromosome she can't exhibit these chromosomes linked genes.

If and when a cross over occurs between the X & Y chromosomes and the particular genes are involved it would be a major break through because now the female would be capable of exhibiting the new gene traits carried in the new X chromosome both with color and caudal size gene traits, plus maybe an additive or cumulative factor similar to the wheat grain color shading covered in part IV. That's why we should not cull too early and not even wait after mating to examine each fish for a possible cross over of a new trait. But realistically, with limited tank space, time and resources, unless the trait is dominant and is seen early, the probability is that most of these fish with new genetic crossovers are culled without realizing their changed genetic potential, and granted not every crossover is beneficial to your breeding goals.

Each pair of chromosomes resembles four parallel strands and as we saw is known as a tetrad. When there is a twisting which occurs in (b) and a crossing of the strands—it results in a mechanism whereby crossing over takes place. Although not documented, I believe there is a static type electrical charge that causes an opposing type attraction of the strands, breaking them apart but not allowing them to flow free (c) and then a recombination as seen in (d).



Vast accumulations of data have now confirmed that such exchanges, or cross-overs, do take place at virtually every meiosis. A study of the percentages of changes that occur in the phenotype enables one to map the alleles on the chromosome and will be covered later.

MUTATION

Any abrupt change in a gene that embodies a new trait and is then passed along like any other hereditary trait, is a **MUTATION** and the organism that carries it is a **MUTANT**. Mutation also refers to the process by which such changes are produced. Mutations may occur "spontaneously" (for unknown reasons) or may be induced by agents that interact with DNA and RNA. Various kinds of radiation and many chemicals that react with DNA and RNA are very potent **MUTAGENIC AGENTS**. New mutations provide the genetic variability used for evolution. Some level of mutation is usually needed to provide the raw material for evolution. Nevertheless, most mutations are detrimental. High frequencies of mutation would thus be disadvantageous to a species, except possibly in a rapidly changing environment. The potential benefits of the use of irradiation (solar irradiation, X-rays, nuclear reactors) must be carefully weighed against the known and estimated potential risks. Similar precautions must be taken to prevent the continued pollution of our environment with mutagenic and/or carcinogenic chemicals. There are risk estimates and precautions that must be taken into account in regard to the potential harm to future generations of living organisms, and we must never lose sight of the increased frequencies of deleterious recessive mutations that may result.

Genes with visible effects or with major effects upon survival and adaptation of the species to its environment are carried in each member of a chromosome pair and are characterized by no appreciable variation. These are often referred to as "**wild type**" genes. However, variant forms of these genes which have no apparent effects on the organism when present in only one member of a chromosome pair are often present in low numbers in wild populations. Genes of this type are **recessive** genes. Dominant genes are those with an observable effect when present in only one member of a chromosome pair. Degree of dominance can vary widely. In some cases it is complete and the outward effect is the same as if the dominant gene were present in both members of the chromosome pair. In other cases dominance is incomplete, with some level of intermediate expression. In wild species recessive genes may exist with much genetic variation. Similarly, for genes affecting quantitative traits in which an intermediate may have adaptive value and for which many gene pairs may affect a given trait, genetic variability usually exists. Mutations may be recessive or dominant, or may exhibit some intermediate degree of dominance. Recessive mutations are by far the most frequently observed type partially because they can be carried for many generations in a hidden form. Often they are brought to light in a species only under laboratory or domesticated situations in which there is some degree of inbreeding. Recessive mutations also occur more frequently than other types. Dominant mutations are observed much less frequently. Those with favorable effects are rather quickly incorporated in a species and thus become the wild type. Those with unfavorable, but non-lethal effects are rather quickly lost from populations due to natural selection. Those with lethal effects do not appear as a phenotype and are, thus, difficult to find. Mutations occur constantly. The average spontaneous mutation rate for a given gene has been estimated to be 1 or 2 new mutations per 100,000 genes per generation. It is reasonable to assume that the genetic makeup of an individual is precise in its engineering and delicate in its balance. If the mutation alters this balance beyond a reasonable limit the organism will usually be unable to fulfill its life supporting processes.

LETHAL GENES:

Another factor that alters Mendelian ratios is a lethal gene or a lethal combination of genes. Although wide anatomical and physiological differences occur within species, there is an eventual limit of deviation from the norm beyond which the organism cannot survive. Death of the organism may occur at any stage of development immediately following fertilization, during embryonic differentiation, at parturition, or postnatally. Death may be due to a variety of causes, such as injury, disease, malnutrition, and harmful irradiations, such as X-rays and gamma rays. We speak of any cause of death as a lethal effect. Any such

gene or combination of genes causes death of the offspring at conception or some time during development because an eventual limit of deviation from the norm beyond which the organism cannot survive was reached. There are some genes which are deleterious to the organism but not lethal, provided environmental factors are especially favorable. These genes are called **SEMILETHALS**. There are undoubtedly many undetected lethal genes, but there are likewise many unexplained deaths due to environmental factors.

The development of a new individual from a tiny fertilized egg is one of the most interesting and complicated processes in all of nature. What any individual will eventually become is obviously dependent on both heredity and environment. Heredity provides the basic specifications, the environment both internal and external, provides the wherewithal with which to fill the specifications. "When an organism succumbs before the usual time for its species, it is often exceedingly difficult to determine whether the cause of its early demise is hereditary or environmental, or perhaps often some combination of these."

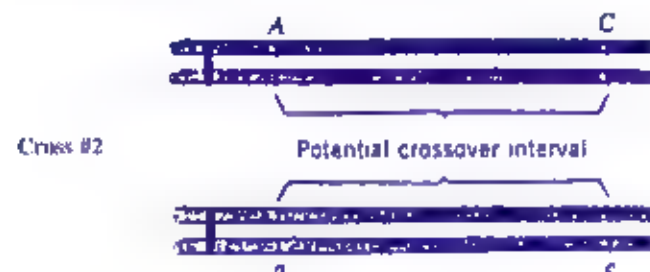
SUMMARY Genes are organized into linear strands in chromosomes. In nondividing cells, the genes remain intact within the nuclei. Genes replicate in interphase of both mitosis and meiosis. Each of the two replicated chains becomes a part of a new daughter cell. Most normal living eukaryotic cells can reproduce themselves by mitosis. Germ cells produce mature sex cells with reduced (n) numbers of chromosomes through meiosis. Through fertilization, a male and a female sex cell initiate reproduction of an entire organism. In development of a new organism, the $2n$ zygote replicates its genes and divides. This process continues and results in the numerous cells that make up the organism. Chromosome mechanisms of the germ cells in meiosis provide the biological basis for the Mendelian principles of segregation and independent assortment. Meiosis provides reproductive cells in haploidy, so that the chromosome number remains constant from generation to generation.

Note: Be thankful we are not working with the genetics of goldfish, because they have 94 CHROMOSOMES.

PART IV RECOMBINATION AND MAPPING

The potential of cross overs is a function of the length of the interval separating the loci. Let us consider a chromosome with three loci: $A \dots B \dots C$. The $A \dots B$ loci are close together whereas $A \dots C$ are quite far apart. A crossover occurring anywhere within the long interval between the $A \dots$ locus and the $C \dots$ locus will produce recombinant combinations: Ac and aC , of the two pairs of alleles segregating in **Crosses #2**. Recombinants Ab and aB will be produced in **Cross #1** only when a crossover occurs within the short interval between the $A \dots$ locus and the $B \dots$ locus. It seems very reasonable, therefore, to expect more recombinants to be produced in **Cross #2** than in **Cross #1**.





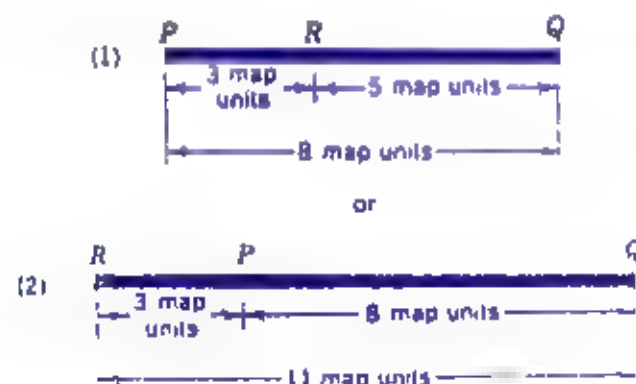
On the basis of the above type logic, one can surmise that the frequency of recombinant gametes produced can be used as an index of the distance between two loci on a chromosome. From this we can determine linkage maps. **LINKAGE MAPS** are made quantitative by defining one map unit as the distance that yields 1 percent recombinant chromosomes or gametes.

It is very important not to confuse the frequency of crossing over, the event occurring in the one tetrad, with the frequency of crossover or recombination chromosomes, the products of crossing over. Linkage map distances are determined by the frequencies of crossover or recombinant chromosomes. Each individual crossing over event yields two crossover chromosomes (two recombinant chromosomes if the interval within which crossing over occurred is flanked by heterozygous loci). Thus, if a single crossover occurs between two loci in 100 percent of the tetrads, only 50 percent of the progeny chromosomes will be recombinant (i.e., the recombination frequency will be 50 percent).

If one assumes that the probability of a crossover occurring between two loci is directly proportional to the distance between the two loci, that is

Probability of crossover = K (distance)

where K is a proportionality constant, then one would predict that map distances would be additive. This property of additivity can be illustrated by the following example. If loci P and R are linked and are 3 map units apart, then loci Q and R are also linked and are either 5 map units apart or 11 map units apart. This additivity can be achieved only by the following two linkage arrangements:



LINKAGE:

Early in the history of genetics it was discovered that not all pairs of genes assorted independently. For example, crosses of purple (dominant) and red gives a 3 Purple to 1 Red ratio in F₁; and crosses of long pollen grains (dominant) and round also gives 3 long to 1 round ratio. It is expected that a cross of purple-long with red-round would give a 9:3:3:1 ratio in the F₂.

Characteristics	Proportion	Ratio
Purple, long	.694	11.1
Purple, round	.056	.9
Red, long	.057	.9
Red, round	.192	3.1

It is evident that these two characters of sweet peas did not follow the second Mendelian law since they did not assort into all the possible combinations in an independent fashion. The two factors from each grandparent—purple and long and red and round—tended to be here together, so that there were more of these combinations than expected in the F₂ generation and fewer than expected of the new combinations (purple-round and red-long). Since the genes tend to stay together, this feature of heredity is called **LINKAGE**. Linkage was not total since some new combinations were formed. Instead of the expected 3:3 ratio, only 9:9 ratio were formed. The formation of new combinations in situations such as this is known as **RECOMBINATION**.

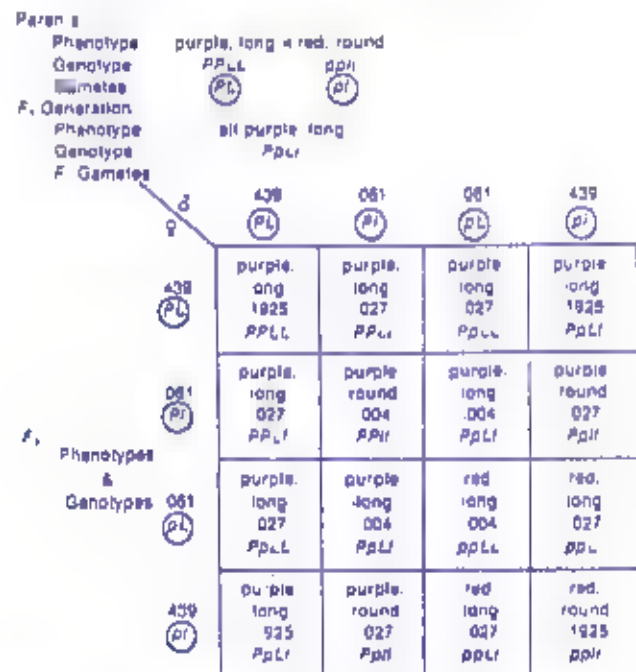
In the case of linked hereditary genes, their behavior in transmission can be explained on the basis of their being located in the same pair of chromosomes, thereby preventing independent assortment, however, since the linkage is not complete, there must be exchange of hereditary material between the two members of the same chromosome pair. This exchange of material, or **CROSSING OVER**, does occur in meiosis and its frequency has been proven to parallel the recombination frequency of hereditary factors.

Specific **ALLELIC** pairs of genes occupy specific positions in chromosomes and recombination frequency is a function of the distance they are apart. Distances are not necessarily standard measurements but are expressed in terms of recombination percentages in the gametes. One way of estimating these is from F₂ phenotype frequencies. As

was stated before, with independent assortment of two pairs of genes, four types of gametes are formed in equal frequencies. Each having an equal probability of uniting with any of the four types at fertilization, the frequency of any of the 16 possible combinations is $\frac{1}{16}$. With linkage the four kinds of gametes are not produced in equal numbers. We can use a diagrammatic representation of the sweet pea example of linkage with the frequency of each combination in the appropriate square shown here.

F ₁ Generation: Phenotype Genotype F ₁ Gametes		$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$
		(PL)	(Pl)	(pL)	(pl)
F ₂ Phenotypes & Genotypes	$\frac{1}{2}$ (PL)	purple, long PPLL	purple, long PPLl	purple, long PpLL	purple, long PpLl
	$\frac{1}{2}$ (Pl)	purple, long PPLl	purple, round PPlI	purple, long PpLl	purple, round PpIi
	$\frac{1}{2}$ (pL)	purple, long PpLL	purple, long PpLl	red, long ppLL	red, long ppLl
	$\frac{1}{2}$ (pl)	purple, long PpLl	purple, round PpIi	red, long ppLl	red, round ppIi

In this case the probable frequency of occurrence is calculated from the red, round F-2 off spring which equals $1/16$ (.0625 divided by 16; .00390625 of the total. To produce this F-2 generation at this frequency it is necessary that the gametes carrying both recessive genes (p) and (l) be present in the frequency of the square root of 0.00390625, which equals approximately 0.039. Because the (p) frequency times the (l) frequency gives us the (pl) frequency is the same as squaring the (pl) frequency, but since we know the (ppl) frequency is $1/16$ we just take the square root of that value. Again from the punnett square we see that PPLl is also $1/16$ therefore the PL frequency must also be 0.039. Now adding these equal values $0.039 + 0.039$ equals 0.078 or the total known frequencies, which when subtracted from a value of one ($1.00 - 0.078$) or the frequencies of the remaining gametes of (Pl) and (pL). Since these frequencies occur equally each must be one half the value of 0.078 or 0.039. Now we can calculate the phenotype frequency observed. That is, 3×0.00390625 plus 4×0.0078125 plus 2×0.00390625 equals 0.0694 which is the frequency of purple, long phenotypes. The frequencies of other phenotypes can be calculated in a similar manner.



The recombination gametes (purple round and red long) when added together and divided by the whole equals 12.2 per cent of the total. Therefore, the genes for color and pollen grain shape are 2.2 crossover units apart on the chromosome.

Obviously it would have been much easier to calculate the recombination frequencies if an F₁ had been crossed to the double recessive ppll. The four possible phenotypes would appear in the progeny in the same proportions as the four types of gametes formed by F₁ individuals. This is termed a **TEST CROSS** and is the usual method of determining linkage strengths. Linkage strength can vary all the way from very low percentages of recombinations if genes are very close together on the chromosome to percentages

approaching the 50 percent recombination which occurs with random assortment. For genes far enough apart that recombination is close to 50 per cent, it is impossible to determine from data on the two gene pairs alone if they are independent or linked. One or more additional intermediate gene pairs would be required to establish linkage relationships.

Linkage is a conservative force in heredity. It does not prevent the formation of new genetic combinations but reduces their frequency because they must then be formed by chromosome breakage and cross-overs.

EPISTASIS:

The interactions between non-allelic genes (those which do not occupy the same position or locus on homologous chromosomes and are separated from each other at meiosis) are called **EPISTASIS**. While it is probably a widespread phenomenon, it must be realized that the expression of any gene in inheritance is dependent upon interactions and interrelationships with others. If one gene of a pair masks the actions of the other we say it's dominant. Likewise, a gene or genes of one allelic pair may mask the presence and actions of those of another pair. Several kinds of epistatic gene action are known, and the epistatic genes themselves may be either dominant or recessive.

If for example we mate a black rat (AABB) (gene A for color, gene a for diluted color, gene B for expression of any color, and genes bb masking all color and being epistatic to A) to an albino rat aabb, all the F₁ offspring are black (AaBb). But in the F₂ generation appear 9 blacks, 3 creams and 4 albinos. This is due to the fact that the presence of at least one A and one B produces black (color and expression for color genes); two a's and at least one B produce cream (diluted and expression for color genes); but either AA, Aa, or aa, together with b's result in albino. This is because the b's mask the expression of A or a; that is, b is epistatic to A or a, so that the last two portions of the usual 9:3:3:1 ratio are thrown together phenotypically. It has been found in all cases studied that genes "unpaired" be involved in specific chemical reactions necessary for development of color pigments. It is not difficult to imagine that there may be a most limitless number of possible epistatic reactions actually present that will continue to interfere with our breeding towards pure strains. Dominance is a hindrance in breeding because it makes it impossible to separate the homozygotes and the heterozygotes by visual inspection. Likewise, epistasis in a hunchbacked breeding since if any desirable qualities of a fish are due to epistatic combinations they may not be passed on intact to offspring because of the halving nature of heredity.

MULTIPLE-GENE HEREDITY:

Suppose we have more than one gene for one color as we increase the number of genes they would have an additive effect on the resultant phenotype color. For example in 1908 Nilsson-Ehle crossed several strains of red and white wheat grains. In general the red color was only partially dominant over white, because in the F₁ the wheat was not as dark a red as the red parent. In the F₂ there were 3 reds (dark red and 2 lighter reds) to one white. This indicated a one-gene pair situation because of the 3:1 ratio. In another cross of red and white parents gave a similar F₁, but an F₂ of 15 reds (of varying shades) to one white, thus indicating a two-gene pair situation. Still a third cross gave the usual F₁, but an F₂ of 63 reds (again of varying shades) to one white. This indicated a three-gene pair situation (3 genes — 64 square punnett chart). In the two-gene pair cross it was shown that a wheat with four genes for red was redder than one with three, this latter one was redder than one with two, and this, in turn, redder than a wheat with only one gene for red. In these cases there is not complete dominance, but the genes act in a cumulative or additive fashion.

MULTIPLE ALLELES:

In the previous paragraphs the different alleles were considered as pairs, or alternate forms of a gene which could occupy a certain spot in a given pair of chromosomes. Alleles also occur in series of two or three or more genes which can occupy a given chromosome locus. These are called **MULTIPLE ALLELES**. However, no individual can carry more than two members of a multiple allelic series. In some cases there are very large numbers of alleles present in different individuals of a population or strain. The best known series of multiple alleles happens to occur in rabbits. If we cross a colored rabbit with an albino, the F₁ are all colored, and the F₂ gives three colored to 1 albino. If we cross a Himalayan, white with black nose, feet, ears, tail with an albino we get all Himalayan and in the F₂ 3 Himalayan to 1 albino. If we cross a colored rabbit with the Himalayan type, the F₁ are colored, and we get 3 colored to 1 Himalayan in the F₂.

From these results in breeding it appears that we are dealing with genes at a single locus having three alternative forms. There are three genes in this multiple-allelic series. Since any rabbit can have only two of them and we know the dominance relations among the three genes, we can derive the possible genotypes of the various colors of rabbits. Let C stand for the color gene, ch for the Himalayan gene, and c for the albino gene.

Colored rabbit	CC or Cch or Cc
Himalayan rabbit	ch ch or chc
Albino rabbit	cc

MENDELIAN GENETICS.

It is now known that many genes are involved in the production of some traits, even though single gene situations can affect basic biochemical reactions and be responsible for alternative final products. It is the genes and not the traits that are inherited. Genes behave as separate units, whereas traits may result from complex interactions involving many genes (single, linked and in different locations and on different chromosomes).

Complete dominance was indicated in all allelic pairs that Mendel worked with and reported on. It was natural, therefore, for him to consider dominance as inherent property of genes. When sweet peas and snapdragons were studied, shortly after the discovery of Mendel's paper, intermediate traits were observed in hybrids. Crosses between homozygous snapdragons with red flowers and those with white flowers resulted in F₁ progeny with pink flowers. Heterozygotes could thus be distinguished phenotypically from both parents. Dominance has now been shown to be influenced by factors in the external, internal (hormonal), and genetic environment. Thus, Mendel's view of dominance as a fundamental, inherent property of the allele alone is not longer applicable for all cases. Dominance of some genes may eventually be explained on the basis of modifier genes that are present in the genetic environment. In other cases, Dominance may depend on the quantity or activity of enzymes that are gene-controlled.

The most important concepts that Mendel deduced from his experiments were **SEGREGATION** the process through which alleles separate and produce haploid gametes, and **INDEPENDENT ASSORTMENT** of different pairs of alleles. These principles are the basic foundation of Mendelian heredity.

IN SUMMARY Mendelian genetics is based on the transmission of chemical units (genes) from parents to progeny and thus from one generation to another. The mechanism of transmission includes segregation and independent assortment. Hereditary mechanisms operate in all plants and animals. Probability is involved in genetic mechanisms and must be recognized in predicting the transmission and expression of both dominant and recessive alleles. Gene product interactions such as epistasis modify pheno-

types and Mendelian ratios.

Genes that are located on the same chromosome do not assort independently during meiosis. Instead, they tend to segregate together. Such genes are said to be linked. By definition, two genes are linked whenever a dihybrid produces over 50 percent gametes with parental combinations of the segregating pairs of alleles and less than 50 percent gametes with recombinant combinations.

Recombinant combinations of genes located on the same chromosome are produced by crossing over which involves the breakage of individual chromatids and the exchange of parts. This process of breakage and reunion is usually associated with a small amount of DNA repair synthesis. Crossing over occurs after chromosome duplication, in the tetrad or four chromatid stage of meiosis. A given crossover involves any two of four chromatids.

PART V INBREEDING

One of the most powerful tools in the hands of the breeder is selection. The use of selection extends as far back as records go in the history of breeding. From successful attempts with improved breeds there grew a belief that selection could improve a breed indefinitely. A selected group of animals or plants thus represents a restricted portion of the total possible range of variation in the species.

Selection is of two general kinds, which in principle are really the same. The two kinds referred to are natural selection and artificial selection. In natural selection certain genetic combinations are preserved because the individuals possessing them are better able to survive through the reproductive period, better able to secure food, more adept at escaping enemies, or better able to procure mates; or perhaps merely because they are biologically or geographically isolated. In artificial selection certain combinations of inheritable characteristics are preserved because they please man's fancy or contribute to his well-being.

It is useless to select individuals on the basis of variation resulting from differences in environment. Such variations, which are spoken of as fluctuations, are not transmitted to the offspring. Selection, then, must be based on hereditary variations. Furthermore, the breed must be heterogeneous as to the character of characters to be selected. When a breed becomes homogeneous as to certain characters, selection cannot change the genetic composition in regard to these characters.

Inbreeding may be defined as the mating of individuals more closely related than the average of their breed or the population concerned. Inbreeding refers to the situation where progeny are produced by closely related parents. **Outbreeding** describes matings between individuals not closely related. It is clear, therefore, that inbreeding may vary greatly in intensity from the mating of individuals that are only slightly related to the mating of those as closely related as father and daughter or full brother and full sister. In contrast outbreeding is the mating of individuals less closely related than the average of their breed or the population concerned.

It is not completely correct to define inbreeding as the mating of related individuals because all animals that can be mated have some common relationship. The degree of relationship for inbreeding may vary greatly. The degree of relationship depends upon the number of genes possessed in common by the two individuals that are mated. It is likely that in the mating of a guppy to a platy the number of genes common to the two parents is not large, comparatively speaking. The number of genes common to both

parents may be expected to increase progressively, from the guppy-patty mating.

What has led to the idea that inbreeding is to be avoided? For one thing, inbreeding seems to suffer in contrast with its antithesis, outbreeding, which in present popular stereotype is usually represented by such mighty examples as hybrid corn and the mule. There are numerous devices among organisms which tend to encourage or to ensure some degree of outbreeding. In many plants and especially among higher animals, the different sexes are always found in separate individuals. This situation precludes self-fertilization, thus serving as effective insurance against inbreeding. Insects must in some form. Even where self-fertilization can take place, ways of forwarding cross-fertilization are strikingly frequent.

Besides these general indications of a superiority of outbreeding over inbreeding, there are numerous specific instances where inbreeding appears to give rise fairly directly to unfortunate biological consequences. For example, we can consider briefly what happens when corn plants are self-fertilized, and then their progeny are self-fertilized, and their progeny's progeny, and so on for a number of generations. Typically, after a few generations the genetic material separates into distinct lines that become more uniform following each self-pollination. Plants with unexpected deleterious characters are likely to appear, such as white seedlings, virescent, yellow seedlings, and dwarfs. Many of the lines die out. Those that survive show a general decline in size and vigor that can be described in measurements utilized for quantitative characters.

We can appreciate, then, why inbreeding has been thought to be biologically undesirable. And we should pursue the matter by asking two questions. Is inbreeding as such directly accountable for the biological evils often associated with it? If not, what is the relationship between inbreeding and its apparently deleterious effects?

You might begin to answer the first question for yourself if you were to take a survey of the typical histories of various organisms. You would find, perhaps to your surprise, that in many successful groups of plants, self-fertilization is the habitual means of reproduction. You would probably conclude that if corn, peas, beans, and tomatoes for example flourish under generation after generation of intensive inbreeding, the practice of inbreeding as such can scarcely be judged harmful.

Your conclusion might be reinforced in various ways. Examination of human family histories would reveal that by no means does inbreeding always lead to disaster. One of the nobler lines of kings and queens known in history, the Ptolemy line in Egypt, was maintained through brother-sister marriages. Much the same lesson can be taken from the experiences of breeders of animals. If you own a fine purebred dog, you need not be astonished to find a good deal of common ancestry in its pedigree. From planned experiments, too, there is abundant evidence that inbreeding does not always produce harmful effects. A clear demonstration of this fact is that vigorous lines of albino rats have been maintained after more than a hundred generations of brother-sister mating.

The facts are that inbreeding does not create any weaknesses or defects. In itself it is not harmful. What inbreeding does is to increase rapidly the homozygosity of the population, to isolate pure lines, to bring to light in the homozygous condition any recessive genes which may have been carried in the heterozygous state in the strain. We now know that most mutations are recessive and that most are harmful. It follows that, because of natural selection, the individuals having the harmful genes in the homozygous state will be eliminated. This leaves however, many individuals in the population carrying one or more of these recessive deleterious genes in the heterozygous state. Under a system of random mating, these are to a large extent carried along, in the heterozygous condition, from generation to generation. Under any system of inbreeding, however, the heterozygotes in the population rapidly become less frequent and the homozygotes more frequent. Since many of the recessive genes affect vigor, fertility, and

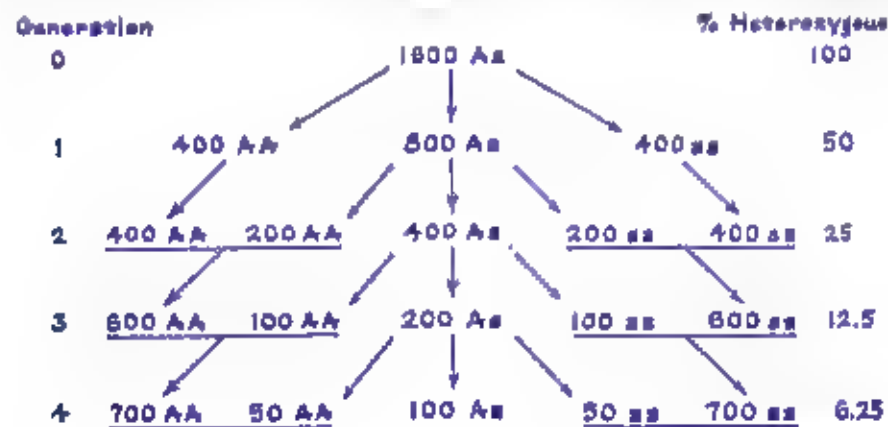
viability, the strain as a whole tends to degenerate under inbreeding.

Not only are deleterious characters brought to light, however, but other genetic characters of the breed become apparent through increasing homozygosity. Some of these characters may be beneficial, or at least not harmful. Thus, if rigid selection accompanies inbreeding, it is usually possible to preserve certain of the desirable combinations in more or less homozygous form. Large numbers of individuals must usually be discarded in the process, however. Meticulous inbreeding with careful selection, has been the basis of building up and improving of most of the modern breeds and varieties of livestock and cultivated plants.

HOMOZYGOSIS.

We can say that deleterious effects seem to follow more frequently on inbreeding than could be expected from mere chance; nevertheless, inbreeding is not in itself necessarily harmful. Further clarification of the situation calls for a closer and more precise analysis. We must turn from a description of end effects to a study of genetic mechanisms. One outstanding genetic effect of inbreeding accounts for many of the other effects associated with it. Inbreeding results in homozygosity, or, if you will, the homozygous state at numerous genetic loci. Let us first consider this principle in its simplest form, by seeing what happens as the result of self-fertilization in organisms heterozygous for a single pair of alleles, Aa. You know that from an Aa cross we expect 1 AA : 2 Aa : 1 aa. For that half of the progeny which is Aa, reproduction through self-fertilization will again give rise to 50% heterozygous offspring and 50% homozygous, with equal numbers of AA and aa being expected. For that half of the progeny which is either AA or aa, however, self-fertilization can produce only offspring that are genotypically identical with their parents. Over a series of generations, then, assuming heterozygous parents to begin with, we might expect that the proportion of heterozygotes would be reduced by half in each succeeding generation. Correspondingly, there should be an increased frequency of homozygotes.

Perhaps you can see this principle more readily after examining the figure below which shows the results of self-fertilization over a period of four generations. Notice that for our simple model, we have made the assumption that each genotype reproduces equally well, a situation not always found in actuality. And if you wonder why we chose 600 individuals to start with, it should be explained that the number is an arbitrary one chosen to permit the expected progeny to come out in simple whole numbers. The results speak for themselves. Beginning with 1600 individuals, all Aa, four generations of self-fertilization will produce a population with 15 homozygous individuals for every heterozygote. A contrast with self-



fertilization over succeeding generations would further reduce the frequency of heterozygotes.

Inbreeding quickly reveals what hereditary traits are carried by bringing to light all hidden recessives. Pure lines are rapidly formed and from these the desired ones may be selected and the rest discarded. Pure lines are of considerable value in many ways. They may be, because of selection, free from defects, particularly hidden defects. They will breed true for all their characters. Since the individuals of a pure line are genetically alike, the modifying effects of the environment may be studied. Variations within a pure line are random genetic. Of course an occasional mutation may occur which will be genetic, but this very fact is of value, since the frequency of mutation may profitably be studied in a pure line. Such occasional hereditary variations are true mutations and not the result of recombinations which often cannot be distinguished phenotypically from mutations in heterozygous populations.

The rapidity with which homozygosity is reached will depend upon the degree of inbreeding and the number of pairs of genes concerned. Self-fertilization will bring about a condition of homozygosity most rapidly. Eight or ten generations of self-fertilization result in an almost complete homozygous condition of even a large number of independent pairs. Brother-sister mating is next most effective, followed by double first cousins, half brothers and sisters, and single first cousins. When the inbreeding is as far removed as second cousins the percentage of homozygotes does not materially increase as a result.

TYPES OF INBREEDING. The expected genetic width between consanguinity is given below with the closest at the top.

Self-fertilization

Full brother and sister or parent and offspring

Half brother and sister, uncle and niece or nephew and aunt

Half uncle and niece or nephew and half aunt

First Cousins

Random mating within a line*

Random mating within a strain† Outbreeding within a strain

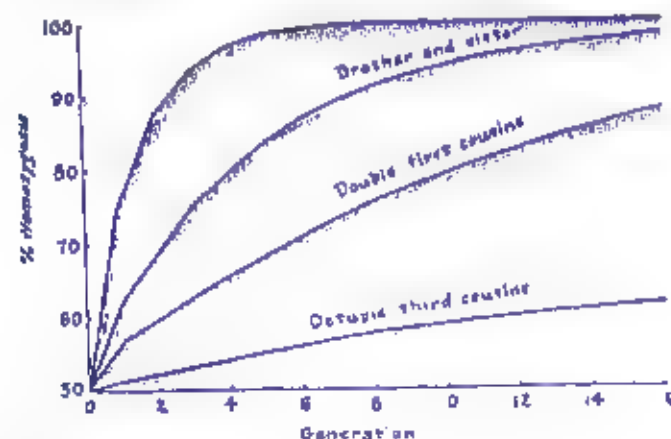
Crossing of definite families within a strain

A cross of strains

A cross of inbred lines different strains

A cross of species

A cross of genera



This type of mating could be much closer than indicated.

The percentage of homozygosity in successive generations under various forms of inbreeding, as indicated by the closeness of relationship of the parents.

At the time of fertilization each of the genes contributed by the female is matched with a gene from the male. The members of a given gene pair may be alike, so that the individual is pure or homozygous for that gene pair, or they may be unlike, so that the individual is hybrid or heterozygous for that gene pair. This situation is extended to the many gene pairs involved. Every mating is therefore fundamentally a mixture of essentially of both inbreeding and crossbreeding, because gene pairings at the time of fertilization include genes that are alike and genes that are unlike.

The mating of related individuals increases the pairing of like genes. The closer the mating and the more often the inbreeding is continued in successive generations, the higher will be the degree of genetic purity attained.

EFFECTS OF INBREEDING

Since inbreeding by promoting the pairing of similar genes increases the likelihood that the new individual will inherit similar traits from its two parents, genetic purity is promoted. Naturally the closer the mating and the longer the practice is continued in successive generations, the greater will be the degree of purification.

Since inbreeding increases the likelihood of similar genes becoming paired, it reduces the percentage of heterozygosity. Inbreeding necessarily promotes the segregation of types, especially during the first one or two generations after a cross. An individual can possess only two genes and a gamete one gene of any particular gene series. When his offspring are interbred the chances that any one individual will receive one or the other or even both of the original individual's genes is greatly increased, and thereby the entire population of descendants will receive more of his genes than is common to the strain as a whole. Inbreeding therefore, automatically decreases the number of genes of any and all allelomorphic series that become incorporated in the inbred strain or family. By the above process the percentage of homozygotic genes is automatically increased.

Another way of putting the same idea, with a slight but important shift in emphasis, would be to say that inbreeding results in the **FIXATION** of genetic characters. To prove the argument in more specific terms, assume a group of organisms heterozygous for two gene pairs (AaBb). Inbreeding might result in the formation of four homozygous lines—AAbb, aaBB, aabb, and AABB. With reference to the characteristics determined by these genotypes, the lines would be true breeding within themselves, barring the possibility of mutation. If a greater number of heterozygous loci were involved in the first place the same principle would still hold. After sufficiently long and intense inbreeding, the population would become separated into genetically distinct groups, each uniform within itself. This effect of inbreeding has implications of prime importance in evolution, and in plant and animal breeding as directed by man.

Increased genetic purification has the automatic effect of generally bringing about an overall reduction in vigor. The explanation for this rests in the causes of hybrid vigor. Inbreeding may be called crossbreeding in reverse. As crossbreeding has the general effect of stimulating vigor, so inbreeding naturally has the opposite effect. Inbreeding automatically increases purification for both the more desirable and the less desirable genes that are closely linked. Such linkage in itself, even with rigorous selection, is sufficient to cause a general reduction in vigor. It is accentuated by loss of the factors responsible for hybrid vigor, such as dominance and, in some cases, gene interaction.

Some breeders have often been disappointed with inbreeding because they seldom obtain as desirable fish from the practice as from outbreeding. The point often missed is that, although it is highly desirable to have inbred lines as desirable a phenotype as possible, inbreeds should be obtained primarily by genotype. **INBREEDING IS A TOOL TO BE USED PRIMARILY FOR THE BUILDING OF DESIRABLE GENOTYPES**, whereas crossbreeding is of special use in the building of desirable phenotypes.

REASONS FOR INBREEDING

The close-bred fish is expected to be the prepotent one. The unusual ability of an individual or strain to transmit its characters to offspring genetically, because it is more nearly homozygous. Being more homozygous a fish will produce germ cells more uniform in genetic constitution. Prepotency is a valuable asset to an individual, a line and a strain. Inbreeding helps to build prepotency.

The first and foremost reason for inbreeding is the purification of the strain. Continued inbreeding when supplemented by rigid selection is the quickest and surest method of fixing and perpetuating a desirable character or group of characters. During recent years inbreeding has been used to develop definite inbred lines which are more nearly homozygous than existing ones, with the expectation that some of the lines will cross to advantage. It is also hoped that the inbred lines will be sufficiently purified to produce a constant amount of advantage from crossing. This approach may be considered an experiment to find a definite method by which inbreeding can be used in constructive fish breeding. It is essentially a copy, with some modifications, of the method that has been used with so much success in corn breeding (See page 89).

Inbreeding is the quickest and most certain method of bringing out what is in a population. Inbreeding brings the recessives to light, many of which are undesirable, thus giving the breeder an opportunity to eliminate them from the population to purify the stock for the more desirable genes.

Inbreeding also breaks up old associations of genes, especially after a wide cross, or whenever a heterozygous population is inbred. As it breaks up old gene associations it brings about new groupings. This process has both desirable and undesirable results. Old associations that led to desirable gene interactions may be lost; at the same time new combinations that result in desirable gene combinations as interactions may follow.

Inbreeding is the only method known whereby purification can be carried forward. An advantage in further purification is that the crossing of more highly purified strains or lines produces more uniform results.

The fundamentals involving inbreeding are rather clear but much is still unknown about its applications. It is far from clear how much inbreeding is needed to obtain maximum efficiency of breeding in crossing. It is probable, however, that the optimum coefficients of inbreeding will show considerable variation from line to line.

Strain crosses appear to offer the greatest opportunity for the development of superior inbred lines. They offer an opportunity for making new gene combinations. The opportunities in this field are practically unlimited, for the genes possessed by guppies are so numerous that it is impossible to estimate the many new combinations that may be brought about.

In corn breeding some desirable hybrids have been produced from very inferior inbreds. A parallel situation may develop in the guppy field, but there are several reasons why it is more difficult for a guppy breeding program to succeed with poorly performing inbred lines.

It is generally assumed, with considerable supporting evidence, that superior traits tend to arise from dominant genes. It would therefore appear that by the development of superior inbred lines more desirable genes would be made pure and retained than by the selection of inferior lines. Thus when the superior lines are crossed more desirable genes should be put in the cross.

A limiting factor to the above reasoning is that gene interaction may make some genes that are undesirable by themselves valuable when in association with other genes. Nevertheless, the limited crossing studies to date indicate that the superior inbred lines and superior individuals on the average produce the best cross-breeds.

EXPERIMENTAL INBREEDING:

Rats having been inbred for six generations, resulted in the average size of the litter being reduced from 7.5 to 3.2. In another case rats were inbred for twenty-one generations and resulted in the average size of the litter being reduced from 6.1 to 4.2. Since these early experimental results coincided so nicely with the popular opinion that inbreeding was deleterious in its effects, the question was for a number of years considered settled. Later Drosophila were inbred and by careful selection a decrease in offspring number was avoided. An interesting point is that when two of the closely inbred strains of Drosophila were crossed, individuals superior in productiveness to either of the inbred parental strains were produced.

A MEASURE OF INBREEDING:

Both breeders and scientists have made various attempts to measure the intensity of inbreeding produced by different systems of matings. An inbreeding coefficient to be of most value should measure as directly as possible the effects to be expected in the average from the system of mating in the given pure strain. The effects of inbreeding are the fixation of characters and increased prepotency; these are in direct proportion to the percentage of homozygosity; the percentage of homozygosity is in direct proportion to the degree of inbreeding. Thus calculating the percentage of homozygosity that on the average will follow from a given system of mating gives the most natural coefficient of inbreeding.

Being related means that two individuals have one or more common ancestors. Actually any two animals in a breed are usually related in this sense. Obviously in a relatively few generations the number of ancestors in the pedigree of any animal is larger than the total number of animals which were alive in the breed at that time. For example, the pedigree of an individual traced back 20 generations would contain over 2 million individuals. Thus in a broad sense, all the animals in a breed are related. With guppies, however, we use the term related in a more restricted sense to mean that the guppies mated are more closely related than average animals of the breed. This usually means that there are common ancestors at least in the first four to six generations of their pedigree. If two guppies had an ancestor in common in the tenth generation, that common ancestor's inheritance would have been halved ten times in getting down through the ten generations to each of the guppies in question. Obviously after ten halvings of that remote ancestor's heredity, the two guppies would have little genetic relationship because of the common remote ancestor. But if, for example, the shared ancestor is only two generations removed, his inheritance has been halved only twice in getting to each of them.

A parent-offspring relationship is the simplest to measure. They are fundamental to all other degrees of relationship as these represent combinations of several parent-offspring relationships. Since half the genes of any animal come from his father and half from his mother, any offspring is 50 per cent related to each parent. Since each parent in turn received half his genes from his parents, and since a sample half is transmitted to each offspring, on the average 25 percent of the genes of any guppy originally came from each grandparent. Again it should be kept in mind that the relationship between two individuals is the extra similarity in the genes they possess due to their common ancestry.

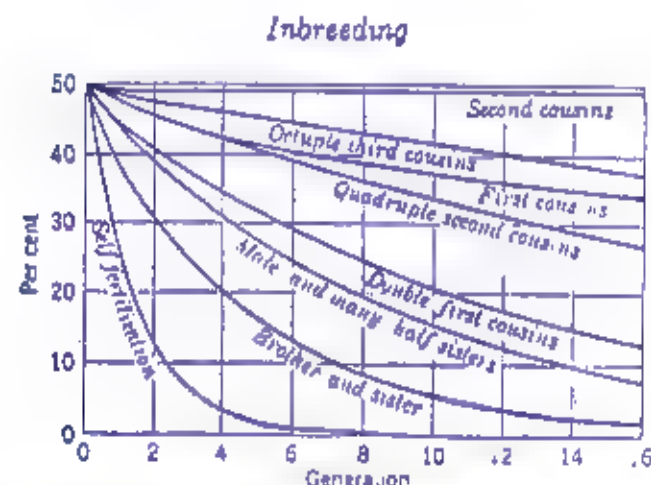
Many of their genes will already be alike because of the high frequency of these genes in the population (strain).

On the assumption that we are starting with a random-bred stock that is 50% heterozygous the below figure illustrates the decrease in heterozygosity in successive generations of inbreeding according to various systems of mating. Although this figure was obtained by theoretical analysis, it coincides nicely with experimental results, as measured by the decline in vigor from inbreeding random-bred stock of guinea pigs.

The coefficient of inbreeding is the measure of the percentage of homozygosity obtained, and is expressed in the following formula:

$$F_x = \sum (1/2)^{n+1} (1 + F_A)$$

- F_x = inbreeding coefficient of individual X
 Σ = summation of all the independent paths of inheritance which connect the sire and dam of X.
 n = number of segregations in a specific path between the sire and the dam of X, and
 F_A = inbreeding coefficient of the common ancestor for each path



Another chart showing the percentage decrease in heterozygosity in successive generations of inbreeding according to various systems of mating

While not everyone is interested in a complex formula, there is such a conclusion arrived upon by controlled breeding and carefully analyzed results. We can interpret the graphs to indicate the following:

- Second cousins will give the same result as random breeding.
- Third cousins will give a 10% reduction of heterozygosity in ten generations.
- A male and many half sisters decreases heterozygosity to 19% in 8 generations.
- Brother and sister give a 10% reduction in heterozygosity in the first generation.

- 20% reduction in the second generation
- 30% reduction in the third generation
- 40% reduction in the fourth generation and decrease in percentage thereafter

Brother and sister decreases heterozygosity to 8% in 8 generations

Self-fertilization would decrease heterozygosity the quickest to 1/2% in 8 generations

HYBRID VIGOR:

Inbreeding automatically reduces the vigor of the stock so bred. It is hybrid vigor in reverse. The constructive breeder then tends to offset this general effect of inbreeding by rigorous selection for improved performance. If the selection is successful, the breeder will hold the performance in balance. It is possible that some highly inbred lines will be developed that greatly exceed good outbred stock in performance. However, this is not likely to occur without considerable effort. It should always be borne in mind that the ultimate objective of the utilization of inbred lines is that they be used in crosses, hence the final appraisal of their value is what they do in crosses. It is doubtful, however, if the benefits from crossing will ever be sufficient to justify the maintenance of lines markedly inferior in performance. Such inbred lines may, however, be used in building other lines that perform satisfactorily. What has been done in corn breeding may be done in constructive puppy breeding.

It has been shown that inbreeding in corn results in various pure lines which by selection may be free from all recessive harmful genes, but which nevertheless, in spite of the best selection, lack vigor. When, however, two different inbred lines are crossed, the hybrid offspring are more vigorous than either of the original stocks from which the inbred lines were derived, in addition to being free from genetic defects. Such "hybrid corn" is of considerable value because of the great increase in yield and uniformity and the freedom from abnormalities.

The large and uniform ears produced as a result of heterosis must not be used for seed, however, as the hybrid vigor declines rapidly in later generations. Instead, the inbred defect-free lines must be continuously re-crossed every year in order to produce the hybrid seed from which the plants showing heterosis are derived.

One good explanation of hybrid vigor seems to be that there exist numerous genes for growth and vigor, each one dominant to its allele for lack of vigorous growth. These dominant vigor genes are scattered on various chromosomes and thus exist in linkage groups. Any inbred line is apt to have some of these dominant genes in homozygous form. Crosses between inbred lines may bring all the dominant genes together in the hybrid, if each inbred line carries the vigor genes which the other one lacks. Thus all crosses between inbred strains do not result in the same degree of heterosis.

On the basis of this explanation, it should be theoretically possible to obtain varieties homozygous for all the dominant vigor genes, so that the heterosis would "breed true." Since, however, there are many such genes, some in one linkage group and some in another, it would not be easy to obtain them all in homozygous form in one variety because of the difficulty of recombining, through crossing over, so many linked genes, none of which is individually recognizable. The best indication that varieties of cross-pollinated species like corn may some day be made homozygous for vigor lies in the fact that varieties of self-pollinated species like wheat and oats are found in nature in a vigorous condition even though they are undoubtedly highly inbred. If nature can accomplish this result in self-pollinated species, man should be able to duplicate it by careful genetic techniques in cross-pollinated species.

Another suggested explanation of heterosis which has received much support is that certain genes in

the heterozygous state result in the production of greater vigor than either allele produces when homozygous. It has been demonstrated on statistical grounds that the dominance hypothesis cannot account for all the observable increase in vigor. Perhaps both hypotheses are correct, and heterosis is the result of a combination of dominant vigor genes and vigor resulting from heterozygosis.

GENERAL CONCLUSIONS:

We may briefly delineate the principles and practices of selection and inbreeding as follows. Selection, to be effective, must deal with heterozygous populations. If the environment is kept fairly constant, the bulk of the observed variation may reasonably be considered to be genetic in nature. Selection must be applied to the individual, not the mass. It must be based on the genotype of the individual, not the phenotype. A definite genotype must be the end in view, usually a homozygous genotype, that is, a pure line. This is most efficiently reached by some system of inbreeding in connection with vigorous progeny selection. After the breed is homozygous, selection can bring about no further advance. Even in homozygous lines, however, selection may serve a purpose, since mutations, chromosomal aberrations, and accidental crossing occasionally occur, producing individuals which are subject to selective elimination.

Selection does not create anything new. It merely sorts out, isolates, recombines, and differentially preserves the genes responsible for the characters selected. Even after a race is homozygous so that further selection is ineffective, however, there may still be room for improvement. New mutations may occur, especially now that the artificial production of mutations is possible, and some of these may be desirable variations. Improvements in the environment, particularly in feeding and rearing, may be feasible. Outcrossing with another breed so as to introduce new desirable genes for further selection may be advisable. Finally heterosis may be utilized in certain cases for increased vigor.

The inbreeding which must so often accompany selection does not create weakness or defects. It merely brings them to light. Crossbreeding, on the other hand, does not eliminate them. It merely covers them up, while still carrying them along. Inbreeding in connection with rigid selection, however, may result in the complete elimination of undesirable genes.

These same principles apply to man as well as to domestic animals, fish and plants.

PART VI CROSSBREEDING

Crossbreeding is the opposite of inbreeding, it promotes the pairing of unlike genes by the mating of different families, breeds, or species. The crossing of individuals that belong to different families within a breed is often spoken of as **outcrossing**, but for our purposes it will refer to crossing between different classes of guppies. Actually the difference between the crossing of families or breeds and the crossing of breeds and species is merely one of degree on a sliding scale. In this respect it is comparable to the difference between inbreeding and line breeding.

Outbreeding is a general term applied to any breeding system in which individuals mated are less closely related than the average of the population from which they come. Outcrossing combined with

selection is a highly useful technique for within-breed improvement for moderately to highly heritable traits. Heterosis is the difference in the performance of the offspring from the average of parental types which is often observed in crosses between breeds, inbred lines, or species. The genetic and physiological bases of heterosis are not clearly understood. Among within-species crosses, heterosis is most apparent for the lowly heritable traits related to fertility and viability. Even though it is not well understood, heterosis can be used to advantage through crossing breeds and perhaps inbred lines within breeds. Breeding techniques designed to increase heterosis or improve combining ability of lines or breed combinations may have increasing applicability in domestic guppies.

The effects of outbreeding are generally opposite those of inbreeding, since with outbreeding heterozygosity is increased. For the most part, the practical usefulness of outbreeding results from the fact that genes with favorable effects generally express some dominance over their alleles. In crossing two diverse strains, lines, or breeds, an increase in heterozygosity is realized. With the increased heterozygosity, "hybrid vigor" is expressed when the average of the offspring exceeds the average of their parents. Heterosis is a more general expression for the difference between the average of the offspring and the parental average, with the potential for positive, negative, or no heterosis. The increase in heterozygosity may promote individual superiority, but it reduces average breeding values.

Inbreeding and crossbreeding are part of the same phenomenon. The results of both are explained by Mendel's laws and the interpretation of hybrid vigor.

OBJECTS OF CROSSBREEDING:

Crossbreeding is the third tool the breeder has with which to work toward genetic improvement. The other two are **selection** and **inbreeding**. Genetic improvement can come only through the sorting out of the genes which produce the most desirable results and by bringing together the gene combinations that yield the most desirable effects.

During the history of animal breeding and more recently the constructive work of the plant breeders have demonstrated that crossbreeding is a **TOOL** to be used for genetic improvement. In general during the past several decades animal breeders and especially guppy breeders have been reluctant to recognize the possibilities in crossbreeding. This situation, however, has been changing with a certain species during the past few years.

Again the chief reason for crossbreeding is to bring about an increase in **VIGOR**. Vigor is used in this instance to cover almost everything that pertains to strain desirability. The main items are **rate of growth**, **economy of growth**, **fertility**, and **general body condition and strength**.

The guppy traits most useful to man may not be compatible with the traits that are most desirable to the guppy under natural conditions. A high degree of fertility is very desirable in the domestic guppy. Under natural conditions a potential drop of 100 fry would decrease the size of the female to such proportion and of such a hindrance to swimming that it would certainly be a liability against predators. The strain that produces fewer number of young, but young that are stronger at birth, may be better suited to survive. A rapid rate of growth is desirable in the production of marketable fish, but in the wild it may be a handicap. The fast growing fish requires a larger daily intake of food than the slow-growing wild fish. Under natural conditions an abundance of food may often be lacking, and the fish with the inherent capacity for rapid growth is handicapped more than the one with less capacity for growth. The same general principle applies to adult size.

The chief reason for including the above at this point is to point out that vigor may mean different

things under different conditions and that it is well to exercise some care in the generalizations drawn from wild types. The fact remains that crossbreeding generally results in an increase in all the elements of vigor, as measured under domestic conditions. A large portion of this increase is due to bringing more dominant genes into play.

It has frequently been stated that inbreeding produces uniformity and crossbreeding produces variability. A statement of this type causes confusion unless it is well qualified. As a rule first and second crosses yield very uniform populations. Inbreeding if continued leads to the development of families and subfamilies the members of which are remarkably uniform, but the immediate results of inbreeding a heterozygous population is segregation of both phenotypes and genotypes.

Crossbreeding promotes the pairing of unlike genes, and it is used for the following reasons:

1. A single cross is used to introduce new genes in a close-bred family. It is a logical procedure in constructive breeding. The quickest and most certain method of improving a trait is to cross breed some stock known to be high in that trait. The argument is often advanced that every strain has all the genes necessary to make within reason whatever is desired from the strain. Even if this statement is correct, it is absurd to take 10 years to do a job that can be done in less time by the use of an improved technique.

The above-mentioned type of crossing, often spoken of as outcrossing and is very familiar to live-stock breeders. It has not been used generally, however, in animal breeding with the deliberateness with which it has been used by constructive plant breeders. The development of improved inbred lines is a most certain to lead to the use of outcrosses for very definite reasons.

2. A second reason for crossbreeding is to make the cross breeds the basis of a new strain. The majority of our present improved strains originated from crossbred foundations. For countless years crossing for this reason has been founded upon in guppy circles, and strain promoters have attempted to prevent evidence that their strain has been pure for years and years. Usually this attitude is the result of presenting only a part of the evidence available regarding both strain history and the history of the human race. It is also the result of a failure to recognize the biological laws of inheritance.

Obviously it makes no difference how long a breed or strain has been bred from within for the value of the breed or strain depends on what can be done with it. Obviously the genes are put in a more heterozygous condition by crossing. Subsequent inbreeding from such a population offers opportunity for segregation. New gene groupings are hereby created, and an opportunity is offered for more desirable gene groupings than existed formerly. Not all new gene groupings will be more desirable. There is no reason why they should be, but by creating new gene combinations the constructive breeder has the opportunity of selecting improved types.

3. The major reason for crossbreeding is to produce a marketable product, advance the strain and obtain show guppies.

HETEROZYGOTE:

As a rule the more heterozygous individuals are the more vigorous individuals. Selection, therefore, especially phenotypic selection, favors the heterozygote. The progress of purification is retarded. The heterozygote can never be fixed but will continue to segregate in the general ratio of 1AA:2Aa:1aa. Since selection favors the heterozygote over the homozygote the population selected as breeders will possess proportionately more Aa individuals. Let us assume 1AA:5Aa:1aa.

Crossbreeding studies are in general accord with theoretical expectations. Crossbreds have usually exceeded the average performance levels of the parental purebreds by margins which are relatively small on a percentage basis for any one trait. Often on a cumulative basis they are large enough to be important in terms of total production efficiency. Increases have been most important for traits most depressed by inbreeding and those expressed early in the development of the individual.

Advantages from crossing of breeds appear to be of sufficient importance, that more breeders should give serious consideration to the development of systematic crossing programs if maximum performance is to be attained.

There are virtually hundreds of crossbreeding systems which could be used. Those most often used include:

1. **Two-breed crosses.** Only first-cross or F-1 offspring are produced with all sold or shown but not used for future breeding. It takes advantage of individual heterosis for vigor, survival, growth, efficiency, or other traits. It does not take advantage of heterosis for maternal traits.
2. **Backcross.** First crosses are made with males for show. Crossbred females are mated to males of one of the parental breeds and all offspring are sold or shown. This system takes advantage of maternal heterosis and of a part of individual heterosis.
3. **Three-breed crosses.** Males of breed A are mated to females of breed B and the resulting male offspring are sold or shown. The A x B females are bred to males of breed C and all offspring sold or shown. The system takes advantage that breeds can be used to complement each other. For example, breed A or B or both can be selected from among those with good maternal abilities while breed C (often called the terminal male breed) can be selected for desired growth, efficiency, and body traits.
4. **Sequence breeding.** Systems in which males of two or more breeds are used in sequence on crossbred female populations.
5. **Criscrossing** is a systematic program with a sequence of two breeds. Males of breed A are mated to females of breed B to produce the first crossbreds. Females from this first cross are then mated to males of breed B to begin the system. In crisscrossing systems a back cross is necessary in the second generation. Nevertheless, in mating crossbred females to males of one of the parental breeds (backcrossing), the first generation crossbred females can express heterosis for maternal performance.
6. **Rotational crosses** is a system of crossbreeding which systematically uses three or more breeds. In a system using three breeds, males of breed A are mated to females of breed B. The two-breed cross daughters are mated to males of breed C. As the rotation continues, the offspring will tend toward having 33 per cent of their inheritance from the breed of their immediate father, 29 per cent from the breed of their second father (paternal grandfather), and 4 per cent of their genes from the third breed.

The offspring from a two-breed crossbreeding system will be expected to express about 2/3 of the heterosis exhibited by the initial crossbred offspring of the two breeds. This follows from the fact that matings will be between purebred males and crossbred females with 2/3 of their inheritance from the other breed. For the three-breed rotational crossing, heterosis would be expected to be about 6/7 of its maximum. Again this follows since the males of one breed are mated to females with 6/7 of their inheritance from breeds other than the breed of their mate.

It is generally recognized that each gene has several divergent effects and that the more favorable effect tends to be dominant over the less favorable effect. Thus, if a given gene affects, let us say, five characters and one of the effects is highly desirable and rather conspicuous, selection is apt to favor this gene even though the other four effects are not revealed because each in turn is covered by the dominant or epistatic effect of another gene. Thus, in part at least, the presence and persistency of lethal genes in guppies may be explained. This fact also supports the theory that it is more effective to select for several traits simultaneously than to develop them in separate lines with the hope of combining several in one line later.

It is quite obvious that a highly heterozygous population offers the greatest opportunity for effective selection. As the less desirable genes become less frequent, selection becomes less effective in that proportion. While the population is highly heterozygous many different gene combinations are possible. Inbreeding tends to encourage different gene groupings. Under these conditions the breeder has the opportunity of selecting not only more desirable genes but also more desirable gene groupings. Selection is most effective when many different gene groupings are being produced. At that time the breeder is confronted with the problem of recognizing the desirable gene combinations when they appear, and of fixing one or several of those combinations. Observation indicates that many would-be constructive breeders fail because of a lack of confidence in recognizing the potential of new gene groupings and the constructive benefits of crossing inbred strains for particular traits.

Selection on the basis of individual merit is strictly phenotypic. It is the most commonly used basis for selective improvement. Undoubtedly most of the progress in guppy improvement to date can be credited to individual selection. Such traits as body type, growth rate, color, fertility, and others of a similar nature can be evaluated directly from the performance of the individual guppy. If suitable performance records are being kept. Such evaluations (or at least fairly accurate preliminary estimates of them) are usually available by the time initial selection of mature breeding stock has to be made. Furthermore, an evaluation of the individuality of all guppies can be made. In contrast, only a few can be properly tested.

Individual selection also has shortcomings which can be summarized as follows:

1. Several important traits are expressed only by males. Thus, selection of breeding females cannot be based on their own performance.
2. Performance records for show qualities are available only after full growth and maturity is reached. (7-10 months)
3. In cases in which heritability is low, individual merit is a poor indicator of breeding value.
4. The easy appraisal of appearance often tempts the breeder to overemphasize this evaluation in selection. (Size vs. carried color traits)

In spite of these shortcomings, individual merit certainly must be considered in selection. In general, for traits expressed by both sexes, only guppies which are themselves above average should be used for breeding, regardless of the merit of their relatives.

Let me emphasize the necessity of basing crossbreeding programs only on purebreds of high individual merit for desired highly hereditary traits. Continuing improvement from a crossbreeding program is dependent on improving the average genetic merit of the foundation strains used in the cross. Selection for heterosis per se has not yet been proven practically successful in guppies. Heterosis among the existing strains should be utilized, however. If improvement above the initial level of heterosis is to be achieved, improvement of the foundation strains must be made. The following figure shows diagrammatically how selection and crossbreeding must be combined to give sustained improvement.

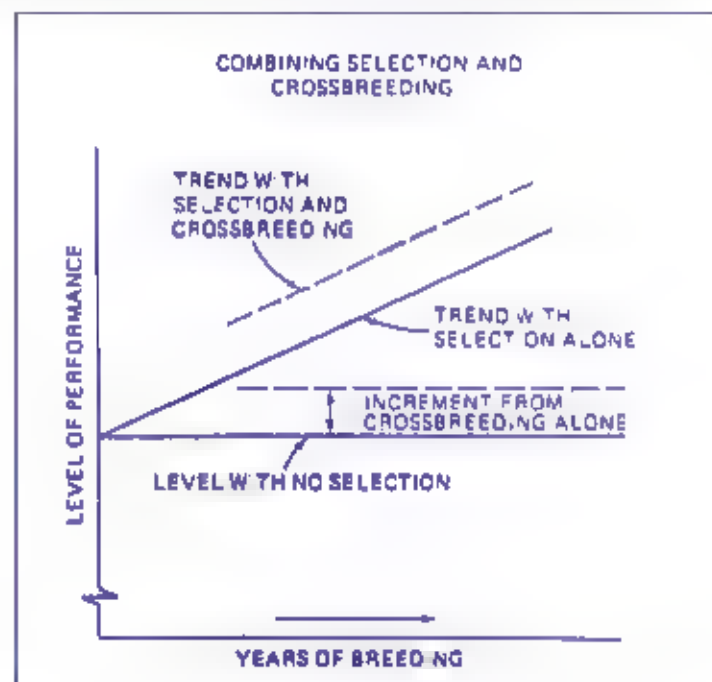


Illustration showing how selection in the parent strains must be combined with crossing to maintain continuing genetic improvement after the initial level of heterosis has been attained from crossbreeding.

GENETIC ASPECTS OF OUTCROSSING

For traits that are influenced largely by genes with additive effects and with a high of selection and heritability, a system of selection and outcrossing would be recommended for most seedstock strains.

High heritability indicates a high correlation between genotype and phenotype. Individual or phenotypic selection is therefore reasonably accurate in locating those guppies with larger than average numbers of desired genes. The outcross mating of selected guppies results in relatively few undesired genes being fixed in homozygous form. A breeding system of this kind brings about immediate improvement and at the

same time does not shut the door on future improvement, as an intense inbreeding program might do through the fixation of undesired or deleterious genes.

LINE BREEDING has been well covered in this volume by other authors and need not be addressed by this author - see index for articles

MAKING GENETICS WORK FOR YOU

by Dr Eugene C. Larr

#reprinted from *The Guppy Roundtable* & forthcoming book
"The Genetics and Breeding of Guppies"

PART I - INTRODUCTION

We guppy breeders are really a class apart, because whether we like it or not we are basically all geneticists. There are those who disclaim the fancy mathematical formulas of genetics, but the fact remains that anyone who consistently breeds his biggest and best male guppy to his kindest female is practicing a form of genetics.

However, the trial and error crossings do not begin to tap the possibilities that emerge from a knowledge of what genes are and how they work. Let's face it, we are lovers of results. And, like it or not, results are a product of genetics. And, as long as we have faced the fact, why not use genetics to help us produce better guppies. There are many ways that an inkling of genetic theory can give us a way to improve dorsal size, body size, color, etc.

This is a series by Eugene Larr on genetics that will go into many aspects of guppy genetics that this author personally has never seen in print. Gene, who is in the midst of writing his own book on guppy genetics, has been raising guppies for 20 years and became an avid gene hunter 13 years ago. He has delved into technical journals from all over the world and conducted countless experiments of his own in searching for the answers to elusive genetics questions.

The purpose of this series of articles is not to teach a course in basic genetics, but rather to emphasize the ways that the principles of genetics can work for you to help develop and improve desirable characteristics and eliminate undesirable ones through the knowledge of the genetics involved with a particular trait.

To refresh or acquaint you with the terminology that it will be necessary to use, we include here a brief rundown on the more important genetic terms.

GENES: The units of inheritance which pass characteristics from one generation to the next. Each guppy has thousands of genes, which align themselves in a linear order on thread-like bodies known as chromosomes.

CHROMOSOMES: All the thousands of genes within a guppy are aligned on just 44 chromosomes plus the sex chromosomes X and Y. Each gene has a particular place on a particular chromosome and controls a specific inherited characteristic.

ALLELES: A given gene may exist in several forms that cause differences in function, color, size, etc. These different states of a gene are called alleles. Alleles always affect the same characteristic and since they occur on the same chromosome, position only two alleles of each gene may be present, one having come from the egg and one from the sperm cell.

DOMINANT OR RECESSIVE: Alleles are classified as to dominant or recessive although some function in an intermediate fashion. An allele is dominant if it can express itself when only one of that allele is present. A recessive allele requires that both alleles be the same before it can manifest its characteristic.

HOMOZYGOUS OR HETEROZYGOUS: An organism is homozygous for a particular trait if both gene alleles for that trait are of the same form. If the two gene alleles differ, the organism is heterozygous (or hybrid).

PHENOTYPE AND GENOTYPE: Phenotype refers to the outward appearance of the individual regardless of genes involved. Genotype indicates the genetic makeup of the individual expressed by genetic symbols.

POLYGENES: Are also involved in the expression of one specific characteristic except that polygenes occur at different locations on the chromosome and more than two can be present. For example, the red color in guppies is the result of the combined action of at least four genes located on various chromosomal sites.

SEX-LINKED: Those traits caused by genes which are on only the X or Y chromosome but never on both. Father to son inheritance is caused by genes on the Y chromosome. Mother to daughter inheritance is caused by genes on the X chromosome. Mother to son inheritance is also caused by genes on the X chromosome.

SEX-LIMITED: Those traits caused by genes which are found in both the sexes but are only visible in one sex. The visibility of the trait being caused by the hormonal balance in the fish.

GENE-LINKAGE: Genes which tend to remain together during meiosis, more because of close chromosomal proximity than because of the characteristic they may affect. Lethally recently gold body color in guppies was linked with shorter, more narrow tails and virtually no gold guppies had long flowing tails.

AUTOSOMAL-LINKAGE: Those traits which are caused by genes that are found on any chromosome other than the X or Y.

CROSSOVER: This is when linked genes break apart and recombine into a new association of genes. In our example of gold guppies, a crossover occurred which broke up the gold body narrow tail linkage so that there are now gold guppies available which are as large as any other guppy. The amount of crossing over is correlated with the distance between the genes involved, with the higher percentage of crossing over occurring when the genes involved are more widely separated on the chromosome. It might be added here that crossovers are very important in guppy breeding. They are what makes it possible to select desirable characteristics individually and separate them from undesirable ones. This would not be possible if genes remained firmly linked, as characteristics would be inherited in large blocks.

MUTATIONS: A gene is an extremely stable unit and can make thousands of exact copies of itself as cells multiply, but occasionally something goes wrong and the new gene differs from the original gene. This mutated gene will now continue to duplicate itself as perfectly as did the original gene. Most mutations are detrimental, but some can be used to advantage. Our wide-tailed guppies of today are a result of many mutations. The heavy tails would actually be detrimental to the guppy used in the wild state, but in this case they are advantageous to us as breeders. Since we can control the environment of our guppies, it

is possible for these wide-finned guppies to live and breed. These mutations are changes of the actual gene structure itself. Other mutations also occur in chromosome structure, but are more correctly called chromosome alterations.

SOMATIC MUTATIONS. Mutations that occur in some cell other than the reproductive cells. As breeders we are not as concerned with these mutations as they are not passed on to future generations. However, they do occur in individuals and are often puzzling.

GENE SYMBOLS: Mendel's method of using letters as symbols for genes is a most universal today. A small letter stands for a recessive gene and a capital letter for the dominant form of the same gene.

PART II - MUTATION

Whether we like it or not, we are basically all geneticists. It is my aim to help you make a better use of the Mendelian laws and in so doing, produce a fish much closer to what you may be seeking.

Let's start off with the example of Mutation. When one is growing a large number of fish there will, from time to time, suddenly appear a different individual. This individual will be so different that it is unlike any of its ancestors. Being different than any of its ancestors of several generations, one can accept it as a mutation and therefore not a product of the normal genetic combinations.

One of the best examples of mutation is the occurrence of the albino in the guppy. In the wild strain of guppies there have been found no albinos. This can be easily understood when one thinks about the survival chances of a white guppy in the wild. Whenever one does occur, it does not live to maturity as it is a sitting duck for the predators in the wild environment. When such a mutation is found in our tanks, however, we can take advantage of it and use it as we see fit.

The albino mutant has appeared several times over the last many years, so that now many of our fish have a gene for albino somewhere in their makeup. Many strains that we find today will throw an albino; this is not new, but only a new combination of the genetic makeup of our complex fish of today. Many authors have stated "The addition of an albino into a strain will give it vigor." While this is not true, it is done by many breeders, which only makes more difficult the genetics we would like to study.

Let us assume that a true albino has appeared in our strain, and we wish to establish a line of pure albinos. In the case of the albino, we are working with an autosomal linkage, and it is visible in the fish regardless of sex. Let us also assume we have a young albino that turns out to be a male. Now what can we do to get a pure strain of albinos going and keep them going?

Let us identify this male fish as follows: he is a phenotype, aa, genotype, aa, and homozygous. We must pick a female for the first cross. She will not be albino and will have no albino genes in her makeup. We will identify her as follows. She is a phenotype, AA, Genotype (AA), and homozygous. Here we are using the type of gene symbols most often used. (AA) is a homozygous gray fish, and (aa) is a homozygous albino fish.

The two fish are put together, and the first litter of young are produced. This first litter will be the first filial generation, abbreviated as F1. All the young from the F1 will look gray, that is, they will be phenotype gray, genotype (Aa) and are therefore heterozygous. We find that gray (A) is dominant over the albino (a), and therefore, any fish with (AA) or a combination of (Aa) will be gray phenotype.

How did this occur? You will remember that during the reduction division in the cells to produce eggs and sperm, there was a splitting of the chromosomes so that each egg and each sperm received one gene of each type. Therefore, in the albino fish the reduction caused each sperm to have only one of this particular

gene for color and in this case it was (a). In the female each egg was given one of her particular gene for color, namely (A). The combinations are therefore as shown below.

		Albino Male genotype (aa)	
		a	a
Gray Female genotype (AA)	P1	A	Aa
		A	Aa

Here we are working with only two genetic elements, (a) and (A), so we have the four combinations shown above. You will note that these are combinations of the single genes from each of the two parents, giving each young fish the required number of two genes for the given trait (color). Many would think that the cross is no good as all the young fish look gray. We can see that they do look gray, but we know from genetics that they are heterozygous, being (Aa), and we can use them for further breeding.

We now have a choice of what to use in the next step of the breeding. We can breed any of this F-1 generation together as brother and sister (full sibling) or we can use one of the F-1 females and the original father (parent x offspring). Let us look at each of these and see what they will produce.

First in the Full-sibling cross we are breeding two heterozygous fish, each having (Aa) in their makeup. Again remember that in the reduction division of these fish, the egg and sperm get either (A) or (a). When the young are produced from this cross, we now have the F-2 generation, some of which look gray and some of which look albino.

		Gray Male genotype (Aa)	
		A	a
Gray Female genotype F1 (Aa)	F1 (Aa)	A	AA(gray)
		a	Aa(gray)

Fish (AA) genotype is gray phenotype and homozygous. Fish (Aa) genotype is gray phenotype and heterozygous. Fish (aa) genotype is albino phenotype and homozygous. Now, what does all this mean. Fish (AA) does not carry any albino gene. Fish (Aa) look gray but carry an albino gene. Fish (aa) is an albino, and therefore carries two albino genes. From this we can now see that we have 75% gray fish and 25% albinos, remembering that of the 75% gray there are 25% homozygous gray (AA) and 50% heterozygous gray (Aa). From here on we can breed the albino fish to each other, and we will get all albino offspring regardless of how many generations we produce, as we have by controlled breeding, dropped out the (A) dominant gene in this 25% of our offspring.

Now let us look at the other way of crossing.

		Original Father Fish P-1, (aa) genotype	
		a	a
Female F-2, (Aa)	F1 (Aa)	A	Aa(gray)
		a	aa(albino)

When the young of this cross are produced, we have a different set of conditions. Although it is a cross of the original father to one of his daughters, we are now working on a new combination which cannot be called an F-2 generation, but must be recorded as F-1 of an entirely new cross. You must make sure in your

notes to make this distinction, as later it will be of great importance.

Now, what do we get out of this cross? Fish (Aa) genotype are gray phenotype and heterozygous. Fish (aa) genotype are albino phenotype and homozygous. In this cross we have 50% grays and 50% albinos. These grays are all heterozygous, having the (Aa), and all the albinos are homozygous having (aa). By crossing in this way, we not only have more of the young albinos to work with, but we have dropped out the homozygous (AA) grays. All of the gray fish can now be allowed to cross, and we know that 25% of all the young will be homozygous albinos.

This technique will be of great interest in some of our other lines of breeding, as it gives us a way to get rid of certain things we might not want. Also remember, we have used the same father, so all of his other traits will also have a better chance of coming through to the young fish. If he has what we want to work on, our strain will grow.

Three laws have now been explained, which we will use many times in later articles. Knowing them well will save a lot of time as we go along.

CROSS	F-1 GENOTYPE	F-1 PHENOTYPE
AA x aa	Aa (100%)	Gray (100%)
Aa x aa	Aa (50%) aa (50%) 1:1 ratio	Gray (50%) Albino (50%) 1:1 ratio
Aa x Aa	AA (25%) Aa (50%) aa (25%) 1:2:1 ratio	Gray (75%), Gray Albino (25%), 3:1 ratio

PART III - SEX CHROMOSOMES

In the last article we went into the genetics of mutation, using the form of albino as an example. In these fish we were dealing with an autosomal (non-sex chromosome) gene which was located on a chromosome other than the X or Y. We must now get more specific about these two chromosomes and how the genetic information is passed through these two bodies.

It is fitting that we talk about the work that has been done on the genetics of the fruit fly as it is from this work that the sex chromosomes were named. It was found that when the chromosomes from a cell were stained and examined under a high powered microscope that the chromosomes were not all alike. There were two which were smaller, and one of these was bent. Further studies revealed that this bent chromosome was found only in male flies. Because of its shape, it was called the "Y" chromosome. Its companion chromosome was called "X". It was also found that when a fly had two X chromosomes it was a female fly, and that when it had an X and a Y chromosome it was a male. From this work the two sex chromosomes were established.

When we apply this information to the guppy, we find the problem not so clearly defined. These two different chromosomes have not been found in the guppy; however, it is assumed that they are present. Many experiments have established that the two chromosomes do exist, although they have never been observed.

With the assumption that the X and Y are there, it is easy to see how the sexes are determined. In a simple cross, without a problem of nutrition, there will be 50% males and 50% females from each batch of young fish.

Using the squares, as we did last time, we find the following. Each sperm and egg get one chromosome from each parent by reduction division. We are limiting ourselves to the X and Y chromosomes, although all the other chromosomes are sorted and passed on to the young just as we discussed last time.

We cannot use the designation of phenotype and genotype as before, so we will designate the fish as follows: the male fish is XY and the female is XX. On the chart we see that the fish have been sexed by possessing the number and types of chromosomes required. That is all XX fish are female and all XY fish are male. Thereby giving us the 50% males and 50% females required.

		Male fish XY	
		X	Y
Female fish XX	X	XX female	XY male
	X	XX female	XY male

When we consider the male and female fish and the chromosomes they have, it is easy to see how certain traits can be passed on in two different ways. In the female fish the presence of two X chromosomes will allow genes to pass from mother to daughter or from mother to son (keeping in mind that each male fish has one X chromosome). But the male fish can pass his genes from father to son by way of the Y chromosome and from father to daughter by way of his X chromosome.

If the gene of a particular trait is located on the Y chromosome, it can only be passed to a male fish. If the gene of a particular trait is on the X chromosome, it can be passed to male or female fish.

If from previous testing, we have found that the male fish is carrying the trait in which we are interested on his Y chromosome, we can breed him to almost any female and his sons will be what we want. This is where the myth got started about the male fish being the only fish that counts in breeding. While this may be true in a few special cases, it is not at all true in the majority of cases.

The most complex system of inheritance are those traits which are located on the X chromosome. In these cases we have a problem in that the female is carrying the genetic information as well as the male, but hormonal differences in the two fish may determine what the fish looks like. It is from this type of genetic problem that we get the two most important forms of inheritance, namely, sex-linked and sex-limited. It is among these two forms of inheritance that we find the most worthwhile breeding in our complex fish of today.

When one wishes to establish or continue a strain, one must first find which of these two forms of inheritance is working. It is only by the use of hormones and/or long breeding studies that one can establish on which chromosome, either X or Y, a particular trait is located. In our next part we will go into the use of hormones and long breeding studies to identify the genes located on the X & Y chromosome and how they affect our fish.

PART IV - HORMONES

There has been a lot of excitement about the use of hormones on guppies. Most of this is because when one uses female hormones, such as **ESTRONE**, in the proper amount, it will make male guppies grow larger and therefore of better size for showing. I believe there is no way of controlling this practice and in many cases there is no way to detect treated fish. When this practice is used for showing, I think it is up to the exhibitor to acknowledge treated fish.

We are, however, talking about the male hormone, **TESTOSTERONE**, or its related compounds, with which we will test our females, such testing can give us information about the genetic traits she may contribute to a given cross. The treating of a male fish with testosterone will do nothing as far as making him change as he already has the ability to manufacture testosterone simply because he is male.

There have been several testosterone mixtures printed in the literature and the one given below is generally used.

0.1 gram of methyl testosterone is mixed into 100 cc of 70% ethyl alcohol. This is then mixed into 900 cc of distilled water thus making our stock solution.

This stock solution will be used in two different ways, which I have called the **SHORT METHOD** and the **DESTRUCTIVE METHOD**. For testing, this hormone should not be added to fish food, as it is impossible to know the amount of hormone the fish is receiving.

We must understand what we are doing to the female fish in this kind of testing. You will recall that the female has no Y chromosome and therefore cannot manufacture testosterone. When this hormone is added to the water in which the female is living, we cause her to absorb it, thus making her cells act as if they were male cells. As the cells react, a change slowly takes place. She will start showing traits she carries, but which may only be visible in the male fish because of his natural ability to produce testosterone.

SHORT METHOD: The female or females to be tested are placed in a small bare tank, the volume of which is accurately known. To this container we will add two (2) drops of stock solution every other day for each gallon of water in the container. We will keep adding this same amount until no more until the female gives the information we are seeking. A calendar is a must to keep a record of the dosage. Females to be used for breeding should be treated for no longer than four or five weeks. Beyond this time she may become sterile. We are looking only for a hint of coloration, so as soon as this appears, stop the treatment. Place the tested female in another tank of untreated water for a rest of about one month before she is placed with the chosen male.

This type of testing is very good for controlled breeding for color of tails and fins. Some females exposed to this test will never lose all their new coloration, but are still all right for breeding.

DESTRUCTIVE METHOD: With this type of testing we will deliberately destroy the breeding ability of the females to obtain the maximum genetic information. A pair of fish are mated and first litter of young are separated, male and female, at about the age of four weeks. We will use all these females for testing. The young females are placed in a small bare tank as before, but we will now add six (6) drops of stock solution every day for each gallon of water the tank contains. With this amount of testosterone in the water as the young females grow, a striking change takes place, and they have developed heavy coloration and a well-defined gonopodium. We now class these females and find what percent of them fall into the different types of characteristics our testing has revealed.

Some time has passed and we now have more young from the original parents. These young have been separated into male and female so that we now have a number of females that can be used in breeding. If in the destructive method of testing, we find that all the females look alike (which is most unlikely) we can choose any female from the new young for further breeding. Generally one finds that only a small percent of the test females show the traits we want, so we must mate the chosen male to a fair number of the new females in order to get the results we are seeking. To further help, we may use the **SHORT METHOD** in all the new females to narrow our selection.

It has been reported that there is a genetic difference in the young fish from litter to litter born of the same parents, however this has not been my experience, and I have often wondered about the validity of such statements. When one is working with large numbers of fish and using virgin females, I don't see how this condition could arise. However, if the female is not a virgin, it is easy to understand how such mistaken and erroneous reports could be made. When a non-virgin is used it is extremely difficult to say that the sperm from a given male is doing all the fertilization. Therefore, it is of utmost importance that virgin females be used in all genetic experiments. The only sure way of obtaining virgin females is to separate all the young fish at birth, each in its own jar, until the sex has been established beyond all doubt. Remember, it has often been truly said that a baby male guppy knows he is a male long before we do.

Experiments have shown that a new male introduced to a previously fertilized female while she is giving birth, will sire some 95% of the next litter. When a new male is introduced to a previously fertilized female three days after she has given birth, about 55% of the next litter will be from the new male. But when the new male is introduced 7 or 8 days after the female has given birth, the new male will have fertilized an extremely small percent of the next litter, and most likely he will have fertilized none of them. As you can see, even under the most ideal conditions, all the young from the next litter will not be fertilized by the newly introduced male. Incidentally, these same kinds of experiments have shown that the female guppy is receptive to the male for only about the first five days of her cycle. As I have said to get the most precise genetic information, we must use virgin females. However, if you want or need to use a non-virgin female, you must introduce the new male as the female is giving birth, then, with him in with the non-virgin female, discard the next three litters; by this time all the next litters will be from the new male. This is an excellent plan to use when one is working with only a few females of a given type.

Next we will be discussing some of the genetic traits which are known and fully understood. Here we will get a glimpse of the breeding and testing techniques necessary to define a given genetic trait and how to use this information.

CAUTION: When we are using these hormone mixtures, we must take a few precautions. Never use any equipment such as a net, dip tube, siphon, or food dispenser in the test tank which you might use in another tank of fish. Keep the test tanks labeled and set aside when not in use, they should be used only for testing. Do not put your hands into the water of a test tank or let the stock solution come into prolonged contact with your skin. Remember, this material is effective in only a few parts per million. Follow the normal precautions of storing the solution out of the sight and reach of children and unknowing adults. I know of no reported mishaps, and if we use some discretion with these materials, we will not cause such an accident to occur.

PART V - ZEBRINUS TRAITS

The trait called Zebrinus was noted early in the genetic history of guppies. This trait is visible on the male fish as a series of vertical pigmented bars located on the caudal peduncle.

We will label the homozygous form of Zebrinus with the code zz . While the heterozygous form will be coded Zz . In this particular case the Zebrinus pattern is visible on the male fish when either the ZZ or the Zz is present. This trait is not visible on the normal female fish. In our study a fish that does not carry any genes of Zebrinus will be coded by zz .

Let us start with a male which is homozygous for Zebrinus (ZZ) and a female which has no Zebrinus in her genetic history (zz). When we mate these two fish we find that in the F-1 generation all the males show the Zebrinus pattern. We might jump to the conclusion that the Zebrinus trait is sex-linked on the Y chromosome because it appears to have been passed from father to son. However this conclusion is wrong. By thinking, we will see our error.

Recalling from the first article that when two homozygous fish are mated, all the young will be alike, and will be heterozygous. In our case all the young fish are therefore heterozygous (Zz). Because the heterozygous or the homozygous form will make the fish look Zebrinus, we can easily see why all F-1 males look Zebrinus (ZZ & zz gives all Zz). The fact that all the fish are Zz can be seen if the females are tested with testosterone, for they will then show zebrinus patterns just like their brothers.

This shows us that the gene for Zebrinus is not sex-linked and located on the Y chromosome, because the female, although having no Y chromosome, shows the trait when hormone tested. Therefore, this gene is located on the X chromosome or on an autosome, and its presence is only made visible by the action of testosterone.

To test the above found facts without using hormones we only need to mate a brother with his sister from the F-1 and observe their young. We find that the young are divided 75% for Zebrinus and 25% for non Zebrinus. Recalling former articles we know that the only cross that will give a phenotype 3:1 segregation, is a cross of two heterozygous fish. We can see from the genetic code that the young fish are 1 ZZ , 2 Zz and 1 zz , therefore, the parents must be Zz and Zz , both heterozygous.

Now that we have found something about the Zebrinus gene, how can we use this information in our genetic study? Let us assume we want to make a new strain of guppies by putting the Zebrinus pattern onto a strain of bronze fish. (The bronze guppy is the type in which the black pigmentation is reduced so that the fish appears bronze. The pigment is not drastically reduced as in the gold and albino types. But, as in the gold and albino types, only the homozygous form displays the trait, while the heterozygous form will look gray in all three types.)

To start, we will pick a male that is homozygous for zebrinus (ZZ) with no bronze in his background. The female will be homozygous for bronze (BB) with no zebrinus in her background. These two fish will have the genetic codes of male $ZZbb$ (the lack of bronze being coded as bb), the female $zzBB$ (the lack of Zebrinus being coded as zz). Keep in mind, that both fish are homozygous for each trait in which we are interested. That is, the male is homozygous for zebrinus and also homozygous for the absence of bronze. Conversely, the female is homozygous for the absence of zebrinus while also homozygous for bronze.

We now breed these two fish and know that all the F-1 generation will be heterozygous (for both traits). Inspecting the genetic code we can see each of the young will be $ZzBb$. Since to look bronze a fish

must have BB in its code, but will show Zebrinus with either Zz or ZZ , the young males when mature, will look gray and zebrinus. The females are also carrying the Zz and when treated with testosterone will look zebrinus like their brothers and will also be gray.

Our next step is to mate brother and sister from this F-1 generation. What will be the results of this crossing? Will we get the type we want, and if so how many? Since we are now working with a complex of two genetic traits, we are faced with the problem of finding the distribution of the genetic codes in this new litter and how this genetic arrangement will effect the appearance of the young fish. There are two ways of solving this problem. One is the use of squares as we did in the first articles. But in our present case, the large square will be made up of 16 boxes, the filling of which is a rather time consuming job, although it gives us the needed information. The other way is a short hand method, which we will use here because it is faster and will be used in future studies. With two traits in each parent to study, we have 16 combinations. Not too bad, but when we are using 20 traits in each parent we have 1600 combinations. It might be fun for some to fill in 600 small squares, but there is a much simpler way.

The short hand method is not difficult to lay out, and I think you will find it a lot of fun as well as see what you can find out in a short time. We will take this first one slowly and explain each part so you can easily see how it is put together. We are crossing brother to sister from our last cross. Both fish are heterozygous with a genetic code of $ZzBb$.

Male $ZzBb$ x Female $ZzBb$

Column #1 (Zebrinus)	Column #2 (Bronze)	Column #3 (Genotype)	Column #4 (Phenotype)	
ZZ	1 BB	1 $ZZBB$	Zebrinus & Bronze	a
	2 Bb	2 $ZZBb$	Zebrinus-Gray	b
	1 bb	1 $ZZbb$	Zebrinus-Gray	c
2 Zz	1 BB	2 $ZZBB$	Zebrinus & Bronze	a
	2 Bb	4 $ZzBb$	Zebrinus-Gray	c
	1 bb	2 $Zzbb$	Zebrinus-Gray	c
zz	1 BB	1 $zzBB$	Non-Zebrinus-Bronze	d
	2 Bb	2 WU	Non-Zebrinus-Gray	e
	1 bb	1 $zzbb$	Non-Zebrinus-Gray	f

In column #1, we are dealing with that part of the cross involving the Zebrinus trait. Since we are crossing two heterozygous fish with genetic codes of Zz , we will get 1 ZZ , 2 Zz and 1 zz . These numbers and code letters are placed in column #1. In column #2 we are dealing with that part of the cross involving the bronze trait. Here again we are crossing two heterozygous fish, with the genetic code of Bb . We will get

BB , 2 Bb and 1 bb . These are placed in column #2 so that each Zebrinus combination has each of the bronze combinations. This allows us to multiply the numbers of each genetic group and place the resulting numbers and genetic codes in column #3. For example, in column #1, we have 1 ZZ , and in column #2 we have 1 BB . This gives us the 1 $ZZBB$ to place in column #3. Again in column #1 we have the same 1 ZZ and in column #2 we use the next group down, Bb to give us 2 $ZZBb$ to place in column #3. Again in column #1 we use the same 1 ZZ and in column #2 we use the next group down, 1 bb , which give us 1 $ZZbb$ to place in column #3. Dropping down to the next number code set in column #1 we now use the 2 Zz against the 1 BB , 2 Bb and 1 bb from column #2. These are computed as before and listed in column #3. This procedure is followed until all the column #3 is filled.

I have added to column #4 a letter following each code group so we might discuss each combination. Fish (a) looks zebrinus-bronze because it has the double code of ZZBB. Fish (b) looks zebrinus-gray because it has ZZ for zebrinus but only Bb for bronze (it needs BB to show bronze).

As you go down column #4 look at the genetic code and see why the fish look as they do. As a last look, fish (c) looks common gray as it has no Z's and no B's, but only z's and b's. Now do you see how we can get rid of genetic traits which are not wanted?

Note also that if you count the total numbers of fish in each genetic group from column #4 (Phenotype) you have the Mendelian ratio of 9:3:3:1. That is, we have 9 fish that look zebrinus-gray, 3 fish that look zebrinus-bronze, 3 fish that look common gray, and 1 fish that looks non-zebrinus-bronze.

PART VI - TEST CROSSES

You might think that our work is finished because we now have 3 fish that look like what we wanted, zebrinus-bronze. But if we are to really make a new strain we must make it 100% pure! It would not be 100% pure as it now stands, as two of the three are heterozygous for zebrinus. We have a segregation of 9:3:3:1 among our young fish, with only four genetic types having genetic arrangements of ZZBB, ZzBB, ZzBb, zZBB. All these fish look bronze and all but one carry the zebrinus gene in either the homozygous or the heterozygous form. This odd fish, zZBB, looks bronze but lacks the zebrinus gene. If this odd fish is a male, we see his lack of zebrinus markings as he matures and discard him. However, this odd fish may be female, in which case we cannot separate her from the other bronze females so easily. Hormone testing would let us find her, but this time we will use test crosses instead of chemicals.

We have seen from the genetic codes that there is no problem with the bronze trait in our fish, as they tell by their appearance that they are homozygous for bronze, which is what we must have. We will now carry out test crosses with all the fish, both male and female. Our problem is, of course, to find those fish that are homozygous for zebrinus (ZZ).

Although I am talking about four individual types of fish, I'm sure you realize that we must have had large number of young so that the laws of chance give us several fish of each genetic type with which to work.

Since the homozygous (ZZ) or the heterozygous (Zz) forms will cause the bronze males to look Zebrinus, we will tackle the male problem first. As I have said before, the bronze males which, upon reaching maturity, show no Zebrinus pattern must be the zZBB genetic form and are discarded. We now cross each of the obvious Zebrinus bronze with females which are totally lacking in the zebrinus trait. Each of these crosses are kept in separate tanks or jars so we can observe and count the numbers of zebrinus males which appear in the test litters. If these males appear at 1/2, the parent male is ZZ and is just what we are looking for. If the young males are 1/4, (Zz, zZ) 50% zebrinus and 50% non-zebrinus... the parent male is Zz and is discarded. This testing has now given us all the information necessary to pick the parent male or males that are homozygous zebrinus, the males we need for our new strain.

We have carried out the testing of the selected females at the same time as we have been testing our males, so we will finish testing at about the same time, and be ready to go on establishing our new strain. Just as you might expect, each selected bronze female is mated to a male fish that has no zebrinus in his background. When the litters come along, the young males of each of each mating are counted and classified as before. If the young males are all Z, the parent female is ZZ, just what we want. If 50% of the young males are non-zebrinus, the female parent is Zz and is discarded. The fish we discussed earlier, the odd one

coded zZBB is now found and discarded as her young males being all zZ (non-zebrinus) have given her away.

Incidentally, all the young fish from these test crosses have looked gray as none of them have the BB required to look bronze. All of these young fish are discarded after we have obtained our information.

We have now tested all our suspected fish and have found which males and females are homozygous for zebrinus (ZZ). These fish are obviously homozygous for bronze (BB). Thus we now have proven ZZBB fish with which to work.

I hope all of you are wondering about our tested and proven females, as they are now contaminated with undesirable sperm from the test males. How can we get these females back so all the offspring will be from our proven ZZBB males? It is at this point that I must explain why I chose to work with zebrinus and bronze types in our study. I've been rather sneaky in selecting these two traits to use in our crosses because it has made our last step very simple, which at the same time gives us an excellent lesson in the mechanics of fertilization.

We know that our proven females are contaminated with the sperm from our test males, whose young we do not want. Let us review, for a moment, this problem of resting sperm in the female fish. The male guppy deposits a quantity of sperm in what appears to be a package. Just how this package is arranged so that individual sperms are released to then fertilize an egg, is not fully understood. But we are not concerned with this package of sperm, but only with a single sperm which might interfere with our obtaining the required ZZBB young fish. A sperm is a closed cell not a small drop of liquid. Some think that there is a sperm fluid that is free to flow and mix with other sperm fluid. **THIS IS NOT TRUE**, and because there is no chance of two sperm mixing together, it is impossible for the genetic information from two sperms to mix. Each closed sperm cell carries within itself its own set of traits coded on its own chromosomes unique unto itself. If the sperm cell wall is ruptured, the cell dies and so does its genetic contribution.

Now back to the problem. We know that the sperm from our proven male is ZZBB, that is, each individual sperm has both ZZ and BB genetic information within its cell wall. Since these two traits are located within each single sperm cell, it is easy to see that when an egg is fertilized by one of these sperm cells, the union must be such that both Z and B are passed to the egg. The egg cells follow the same rules, and in our females we know that both the Z and B must be enclosed in each egg.

Now with the above in mind, we can mate our proven males to our proven females and completely ignore the contaminating sperm. In the first several litters there will appear some gray young fish which came from the sperm of the test father and are discarded. All the young that look bronze at birth must be the product of a union between the ZZBB male and the ZZBB female. By this last segregation we have reached our goal and all the young from our proven parents, which are homozygous for both zebrinus and for bronze, give us a 100% pure strain.

You can now see how the use of genetics will allow you to produce any type of guppy you want in the shortest possible time. Considering your own particular desires, if you are starting to work with a pair of new fish, the genetics of which are unknown, it is by observing their offspring that you will get the information you must have to use the new parents to their fullest potential.

PART VII

SOME BREEDING THOUGHTS PLUS A DELTA TAIL STUDY

In the last articles we have been talking about how one can cross fish in such a way as to produce a new strain. We have seen how to identify the parent fish as to homozygous for the two traits in which we are interested and thereby produce a new 100% pure strain. I would like to mention one other technique supposedly used to establish a line of new fish. Using the strain we have just studied, the zebrias-bronze let's look at the highly publicized technique called "Population Establishment". In this method we are told that six males and a dozen females are placed in the same tank and are allowed to cross at random. The young are collected and reared as we can go to the next step. This step is, of course, the same as above, six males and a dozen females are placed together and so on until we supposedly reach an established strain. Using our zebrias-bronze fish we know that all the young look bronze, so we are ahead on that point. But the other trait, zebrias, is not that simple.

Let's look at the result of their random crossing. We know that ZZBB males to ZZBB females give us all males showing Zebrias and all females homozygous for zebrias. We also know that a ZZBB male to a ZzBB female gives all zebrias looking males, but males and females alike are a 50-50 mixture of homozygous and heterozygous zebrias traits. We also know that a ZzBB male to a ZzBB female gives us 25% homozygous (males look Zebrias), 50% heterozygous (males look zebrias), and 25% homozygous for non-zebrias. We know that the Zz male to the ZZ female gives us 50% homozygous and 50% heterozygous (all males look zebrias). Remember our odd fish, the female zxBB which we could not easily find? If a ZZBB male finds her, we have all heterozygous young (all males look zebrias). If a ZzBB male finds her we have 50% heterozygous (males look zebrias) and 50% homozygous for non-zebrias. You will note that all along the way we could discard all the zxBB males as they do not look zebrias. But the zxBB females remain undetected to do their dirty work. It must now be plain that using the "Population Establishment" method, we would never know which fish are the desirable parents to produce the 100% pure strain. We do now have a tank with a great number of zebrias-bronze looking fish, but we had none when we started.

The example we have just studied must make it clear what a hopeless condition might exist if we try the "Population Establishment" method on a truly complex fish. Our zebrias-bronze was complex, yes, but nothing compared to today's fish. Think of what a genetic complexity you would have trying to work on a green cobra with a red tail and a red dorsal fin! When you try the population establishment method, you will have many fish, some of which may be beautiful, but please don't pick the best from these tanks and delude yourself and/or others by saying that "Here is a new strain that I have established." If you will do your genetics work carefully and with a little patience you will soon be able to say, "Here is a new established strain" and mean exactly what you are saying.

#Reprint editors note: For clarification if we begin with proven ZZBB males and females, there can be no problem because a (z) or (b) can not materialize out of nowhere. However if we begin with only phenotypic zebrias-bronze looking fish, that is where the problem comes into play - who is Zz, ZZ or zz in the female and Zz in the male? But the object of the "Population Establishment" is to produce a sturdy strain with random breeding of chosen breeders - not to develop a strain from doubtful genotypes. It should diminish the mistakes you might make by choosing a wrong single male to improve your strain after you have established this population then go on to selective Line or Inbreeding.

In order to start exploring the genetics of the Delta Tail Guppy, let us look at a physical condition we see in this type of fish. In my opinion, a Delta male which is forced to swim in an almost vertical position or at a 45 angle is not a good-looking guppy, no matter how wide his tail or what color it displays. Simply by looking at the deltas display at any show will quickly show what I am talking about. A recently finished project may give you some food for thought. Ten male guppies, which were the best deltas that could be obtained, were used for an anatomical study. The first thing noted was the great difference in angle at which the fish normally swim. The second factor noted was the great difference in tail thickness in these fish. Each male delta was measured for tail thickness using an optical micrometer. These measurements were taken at the midpoint of the tail, between the end of the caudal peduncle and the end of the tail itself. Measuring through the tail just as if you were measuring the thickness of this paper, the measurements taken in thousandths of inches gave a range from a minimum of .0045" to a maximum of .028". I suspect what I am going to say the delta with the tail thickness of .0045" could swim in a perfectly normal manner. (The breeder tells me "This type can easily fertilize a female even when he is fully matured.") The angle of tail drop is directly proportional to the tail thickness, so that the male which had a .028" tail thickness could not swim horizontally at all. (The breeder tells me "This type must be raised very early because when they mature, the males are no good for breeding.") I noted, in fact, that this male .028" tail thickness could only swim in a straight line when he headed down toward the bottom of the tank.

We must be careful in breeding very young fish, as it is only in the adult form that genetic information can most fully express itself. With the above in mind we must be doubly careful when breeding for our superb guppies or we may lose the very thing for which we are looking. This is just one of the situations which, overlooked, will cause us big problems in breeding delta guppies.

In studying the genetics of the delta, in I, it has become increasingly apparent that the responsible genetic traits are extremely complex. Part of the genetic information is located on the X and Y chromosomes, but most of the important factors are located among the autosomes. We know that deltas carry genes for double sword (DsDs) and caudal pigmentation (CpCp). With this in mind we can say that a delta is a fish which has DsCp in its genetic code. What about the angle of spread between the top and bottom edges of the tail? At least one of the genes and/or its modifiers, is located on the X chromosome. Now, if we have a very good delta, he is DsCpAs (at least), with the As being on the X chromosome which he carries.

From a former article you recall that a young male has only the X chromosome from his mother - a young female has the X from her father. If the fish you use for parents do not have the right combination of male and female X chromosomes, you will have lost the genetic delta. Therefore, when breeding a very good male to an unknown female, it is imperative that you breed father to the F-1 daughters, for some of these will be nearer the right combinations.

It is known that there are several different genetic combinations that make up the different strains of delta guppies. It is because of this that we are often disappointed in crosses between different strains. If we breed two strains that are compatible, fine, but if the strains are not compatible - disaster. It is from this latter type of outcrossing that genetic monsters are formed. They may be good looking and good show fish, their genetics is so mixed up that it would take many generations of inbreeding to establish a new strain. We also find another interesting point, in the delta guppy in that there are some strains in which the male parent seems of the most importance, while in others the female is the major genetic contributor. We have just begun to look at the genetics of the delta and we have a long way to go.

PART VIII

DELTA TAILS, THE FEMALE

When we select parents for a cross to produce delta tails, we must pick the male and that female which are genetically equipped, as well as genetically compatible. The male parent seems rather easy to pick because of his appearance. The female, however, is another question. Let us look around and see what we can find out that might help us answer this question.

First let us look at the females used by several breeders of deltas and see if there is any correlation between her tail shape and the tails of her male progeny. Picking three breeders of deltas that have consistently produced fine males, we will explore this problem. Let us call them strains A, B and C for the sake of clarity. I think it only proper to quote the descriptions these breeders gave me in regard to their females. Breeder A, "The females with large box-like tails which are almost delta themselves throw my best delta males." Breeder B, "The best female to give delta tail young, is one with a dark large fin with a good shark fin point on its top rear edge." (The reference here to the "dark" in breeder B's fish is due to the strain which is a very dark blue-black.) Breeder C, "Females which give me the best deltas are big, well-shaped and have clear, large round-tails." As you can see from these few remarks, we don't even seem to have a good guide for picking the right female.

Bearing a group of young from each of the above strains, we examine the results to get some hint as to the most desirable tail shape for the fertile parent. Carrying out sibling crosses within each strain and tabulating the kinds of young males, we find the following:

Strain	Cross	Delta	Wide-tail	Reject	Total
Box-tail	A x A	20	23	7	50
Shark-tail	B x B	16	23	11	50
Round-tail	C x C	34	6	10	50

The above collection of male fish were examined at the age of nine months so correlations could be made on adult fully-developed guppies. The total of 50 males were all taken from the same male and female sibling parents within each strain so we would not be hindered by the smaller genetic variations which are present in sisters and brothers of the same strain.

(The material was composed as only a small part of the study on deltas. The test was as follows: eleven strains were observed for purity. The three most pure strains, each with a different female tail type were selected. Eight pair from each of the three were taken for breeding. Each of the eight pair were allowed to give equal numbers of young. The total number of young observed as 2,584. I choose only one pair from strains A, B and C, along with their simplified data for this article. This data simplification did not change in any respect its value, nor did it in any way alter the overall analysis. Since I felt the overall sample adequate, I also feel that these fish were typical of the strains in all respects. No one can say how the figures would stand against a breeding test of 25 or 50 pair from the same strain, but until someone does that great amount of work, I feel justified in considering my data valid. The figures and percentages were very close, much closer than anyone would like to work with, and it was only after observing the great consistency of these figures throughout the test strains that I mention them at all.)

The preceding table shows that strain A produced 40% deltas and strain B produced 32% deltas, while strain C produced 68% deltas. Along the same line of thinking, strain A produced 46% wide-tails, strain B produced 46% wide-tails, and strain C produced 3% wide-tails.

We can also group the deltas and the wide-tails together and call them "fine guppies." We then see that A produced 86%, B produced 78% and C produced 80% "fine guppies."

As we study these percentages, it is quite clear that strain C is the best for producing deltas, with strains A and B following. Now, if we look at the "fine guppies" we see A the Best, followed by C and B.

While the spread percentages is obvious in the delta-producing females, it is not so great in the "fine guppies." Therefore in the matter of deltas, C is certainly the best, while in the "fine guppies" A is best, followed by C and B without much spread. However, since we are interested in deltas in this study, we must conclude that the round-tail C is the proper way to go. A is not so bad, but B should be looked upon as a not-too-promising female to explore.

I believe it goes without saying that strain A is certainly the most well-established, having the least number of rejects, while strains B and C appear to need a little more work. Had all strains produced the same numbers of rejects, or none at all, the test would have been more meaningful. However all was not lost, for by observing the sisters of all the male fish we've studied, a very interesting conclusion was noted.

Examining the tails of the year-old females from each of the strains, regardless of their basic tail shape, it was found that there was a thickening of the upper and lower caudal fin rays. These females were examined against a brightly lighted background so that the actual color caused by caudal pigmentation, could be ignored in dark-tailed females. This observation can be quite difficult. When this fin ray thickening was noted, a quick count of these females revealed almost the same numerical proportions as noted between the rejects and the "fine guppy" males. Strain A had eight females without this thickening, strain B had none without this thickening, and strain C had eleven females without the thickening.

With the above in mind, I checked with a few of the local breeders working with deltas and found in most cases the upper and lower caudal fin ray thickening was visible in their best females. While it might be completely wrong and misleading to say that here is a way of selecting delta-producing females, I think we should examine our females more closely.

Since we know that the majority of the genes giving us the delta guppy are located on the X-chromosome, possibly the female is displaying some of these in her tail. I would suspect that she might be partially displaying the double sword complex, which we know to be autosomal.

To add one more thought to this female problem, let me put forth the following: You are just getting started in the breeding of deltas, you have purchased a trio of good looking fish, and the breeder or shop from which you obtained you fish told you "You will probably get the best delta young by breeding to a female with a large box-tail." With this in mind, you select your females for box-tail shape and continue a program of breeding selecting always box-tailed females for your female parent while also selecting your best males. Now, as we look at your established, or nearly established, strain, we note that your good females are indeed box-tailed. This sort of observation, after a long line of breeding, is just the sort of thing we would expect. When we realize that the genes controlling the tail shape of our females are not necessarily the same as those we see expressed in the male, it is quite easy to be selectively breeding in two directions at the same time.

PART IX BREEDING PROGRAM #1

Let us depart from our study of genes and genetic locations in the guppy, and explore the different facets of breeding. This may be of more immediate interest, as it is a constant concern to the beginner as well as the advanced breeder. However, let us not forget the genetic ground we have covered, for it is by knowing what to look for and what to do about what you see, that rapid advances can be made. To impress this thought on your mind, let me quote from Dr. Myron Gordon. In his book *GUPPIES AS PETS* he states, "You do not have to study Dr. Rice's 750 page book to breed guppies of your choice, but chances are that you would be a better guppy fancier if you did" (Dr. Rice's book is *BREEDING AND IMPROVEMENT OF FARM ANIMALS* which was published by McGraw-Hill.) Just in passing, *GUPPIES AS PETS* should be in all our libraries.

There are three major types of breeding:

1. INBREEDING
2. LINEBREEDING
3. OUTBREEDING (Outcrossing)

The first, **inbreeding**, can in turn be of three types, father to daughter, mother to son, or brother to sister. The second, **line breeding** is usually that of breeding cousins, but it can also be the breeding of a half-brother to his half-sister or vice versa. While the third, **outbreeding** is a crossing between two completely unrelated strains of guppies.

Inbreeding is the best way to proceed when one is establishing a strain or sorting out deviations from a particular strain. To illustrate this form of breeding, let's take a pair of fish (closely related) from which we wish to make all the young males look like the father. We often hear breeders remarking that they obtain eight or ten matching males from a series of young taken from the same parents. This number can be greatly increased through careful breeding.

For the sake of simplicity, I will use capital letters for each fish and for each young produced by the cross. As mentioned above, we have two fish to use as parents, **A** is the male and **B** is the female. The young will be **C** for males and **C** for females. You will note that all male fish have a bar beneath their letter and that the letter representing the young from the cross is simply the next available letter in the alphabet.

A x B gives us **C** and **C** young. As we examine **C** when mature we note that only a few of them look like **A**. If we are searching for **A**, then we must now cross **A x C**. This is done because **A** of course, carries the set of genes we want. We know that the **C** does not carry the **X** chromosome of **A**. We also know that the **C** does carry the **X** chromosome which was passed on to **C** by **A**. The **Y** chromosome was passed from **A** to **C**, so that part of the genetic arrangement is known. Since the segregation of the autosomes follows a similar pattern, we can use the same concepts for these as we use with the sex chromosomes.

Our next step, **A x C** gives **D** and **D**. Here again all the **D** do not look like **A**, so we keep going. **A x D** gives **E** and **E**. By this generation we should be well on the way to producing a lot of males that look like **A**. Once we have reached this level of purity by back crossing, we can then start breeding brother to sister generation after generation as long as you like.

If during our breeding, **A** dies, we must pick a male from **C**, **D**, or **E** that is most like **A** and continue breeding. The death of **A** will slow up our rate of establishment, but we can go on working and will arrive at the desired point. In thinking about this back breeding to **A**, please bring to mind article number II and note the percentages obtained when we made sibling crosses (25%) and when we made back crosses to the original father (50%). By noting the changes in the genetic arrangement you can easily see the reason for breeding back to **A**.

Before closing this article I should like to direct your attention to a condition we hear about all the time, namely the weakening of a strain by close inbreeding. The weakening of inbred fish has been observed many times, but the cause of this weakening is not as obvious as some would have us think. You will notice above, when we looked at **C**, I mentioned we observe the **MATURE C**. That is exactly what I meant, for it is only in the mature fish that we see what that fish is really like. The breeding of young fish as soon as they show their colors is very dangerous, because it is under these conditions that we overlook the weak and undesirable traits, and somewhere down the line we find that our strain is no good. However, don't say "inbreeding too closely for too long has ruined my fish." Because **YOU RUINED YOUR FISH AND YOU DID IT BY IMPROPER SELECTION** - the inbreeding only made your mistakes apparent.

Undoubtedly one of the best examples of this kind of error is that genetic combination which manifests itself as a **deformed or curved spine**. I am amazed to constantly hear "My young fish look very good, but as they grow they develop deformed spines to such a degree that they are no good at all." Then to my stunned amazement he will continue "I think I'll take one of my young males while he still looks good and breed him to some females from a friend of mine so I can add new vigor to my strain and have better fish to work with." If this breeder thinks his good-looking young fish is passing on a different kind of sperm than when it is an ugly fish, he had better change his way of thinking - breeding and selecting for his fish will quickly be right back in the same ruined condition.

I'm sure that from this single example you can see what I am talking about, and if any of you are in such an unfortunate position, I hope you now see how you got there - and how to correct it. Those of you fortunate enough to hear Dr. W. H. Ruedemann speak on genetics, will recall his comments on the successful inbreeding in the 20th generation and beyond. He also pointed out that after such a long breeding program, the genetic structure of the fish is so stabilized that mutations cause most of the observed deviations from purity.

PART X BREEDING PROGRAM #2

A number of readers have asked how I chose the young females to use in the backcross we started last. Please look back to **Article IV** (p. 98) that part on hormone testing. Quickly recapping: all the first litter females are tested to **DESTRUCTION**. Keeping wary records of these fish, we note those early changes which were indicators of the change seen in the fully masculinized females. With this information, the second litter females (from the same parents) are tested by the **SHORT METHOD**. When the noted indicators are observed, the desirable females are placed in a fresh tank for a month's rest, after which the cross is made. You say that this takes too long... well, it does take time, but with this kind of testing you will not be burdened with a great many young that **YOU HOPE ARE GOING TO TURN OUT THE RIGHT WAY**.

The same method of backcrossing to an original female is used (as was shown in backcrossing to an original male). When we backcross to the mother, however, we must take great care to be certain that the new son is really siring the young. Read the latter part of Part IV) (p.99) Backcrossing to the original female is the most time consuming and difficult form of crossing. However, in many lines it is the only way to obtain the desired results. The black guppy must be approached in this way.

Let us set up the following from the offspring of A x D (which gave us E and F) we pick two pairs. Keeping the designation of E and F for one pair we designate 2 E and 2 F for the second pair. This way we can tell at a glance that we are running two lines of the same generation of the same strain.

Each of these lines are kept separately and extended by the use of sibling crosses, constantly using great care in selecting the parents for the next generation. In this study we will not select for the same traits in each of the two lines. In a few generations of inbreeding we have two separate lines, closely related, but no longer brother and sister.

PART XI LINEBREEDING

To bring our breeding steps to date into a more visual pattern we can diagram them as follows:

A x B Original cross — C

A x C Backcross — D

A x D Backcross — E and F

We were pleased with the results of this last backcross and started inbreeding by siblings. We had set up two lines of this strain E, so we will continue this by the number 2.

E x E	2 E x 2 E
E-2 x E-2	2 E-2 x 2 E-2
E-3 x E-3	2 E-3 x 2 E-3
E-4 x E-4	2 E-4 x 2 E-4

Here, as per our code, we see that our sibling crosses within the two E lines have been carried to the 4th generation.

The act of LINEBREEDING is a cross between these two very closely related lines. These closely related lines are, of course, E and 2 E. Also, we see that E and 2 E were brother and sister, and that 2 E and F were likewise brother and sister when we started the inbreeding. We can see that E-4 and 2 E-4 generation are not brothers and sisters.

To make a linebreeding cross we simply select a male fish from E line after the second generation and a female from 2 E line also after the second generation. These crosses can be made across the same generation level or can be made up and/or down between the two lines. For instance E-4 x 2 E-2 or any combination as long as it is across the two lines we have set up.

Here again we must change the codes for the young of these line-crosses because we are no longer inbreeding. I have shown two types: E-4 x 2 E-4 will give F and F, while E-4 x 2 E-3 will give G and G. If these letters F and G have already been used for some other set of crosses, just pick the next available letter. When you reach Z, the next code is AA, AB, AC, etc. through AZ, then BA, BB, BC through BZ, etc. This allows over 700 designations through ZZ, and if you need more simply double the first letter: AA, AAB, etc. This system allows you to go back through your records and construct a complete family tree of any one fish. NEVER REPEAT CODE SETS! SOMEONE, YEARS FROM NOW, MIGHT NOT UNDERSTAND WHAT YOU WERE DOING. (and this someone may be you).

Line breeding can be made in more complex patterns than the type I have illustrated, and a quick look at a text book on genetics will show you the other forms. Even though you will be reading about rats or fruit flies, the same geometry of linebreeding patterns applies to guppies.

The purpose of linebreeding is to maintain a strain of fish by allowing you to breed between closely related lines. This works very well in most animals, but I personally never use it with my guppies. I find that with proper selection, a series of continuous inbreeding will not cause any problems. I have seen many times a breeder setting up double lines to preserve his strain by linebreeding, only to find, after several generations, both lines were showing the same undesirable condition. Why were both lines showing the same problem? He had used the same incorrect method of parent selection in each line. One line went bad, can we expect the other line to be any different? My advice here is not to worry so much about all the bad things you heard about inbreeding, and take a little more time to **REALLY CHOOSE THE RIGHT PARENTS!**

Glance back to part IX, last paragraph. One could never reach the 20th generation of inbreeding if we heeded the warnings against inbreeding; all the fish should have been sterile long before such a point was reached. You must realize that inbreeding to the twentieth generation takes a good many years, so don't be misled by someone who, after four or five generations of inbreeding, tells you that this is the worst thing you can do. Instead of being misled, just ask one simple question, "How do you select the parents?" Then if you cannot see what went wrong, my articles may have missed their point.

Let me quickly say...I do make mistakes, and a lot of them. I do not imply that my methods are infallible, but when I do go in the wrong direction, or make a mistake in selection it does not take long to realize what I did wrong and how to correct the error. This is why I keep harping on keeping good records. Without proper records I could just keep stumbling around in the same mistake which is a great waste of time, patience and money.

Because of my strong feelings about the value of linebreeding, I request that you look at the October 1967 bulletin of the SGVGA and read the article "Linebreeding" by Midge Hill. This article will show you how you can use linebreeding in your individual set ups. It will be obvious that Midge and myself do not agree on the use of this breeding technique, but between these two articles you may be able to choose for yourself.

TIME NOW FOR A FEW ANSWERS AND COMMENTS:

"How long do my males live, and do I keep them in suspended animation?" First, let me say, if you want to do serious genetic work, the fish must live and be sexually active for about two and a half years. No, no suspended animation, but wouldn't that be wonderful? There it is, at this time swimming in my tank #48-10 some males that were born October 12, 1964 (date of writing this is January 1969). If I count right that is 50 months and sixteen days. Sexually active? Yes, their last young were born November 10, 1968.

from virgin females. The answer to all of this is a simple one: **DO NOT FEED YOUR FISH TO DEATH!** Many have criticized my feeding ideas, saying "that's not the right way to do it." However, I think my 4 year two month old fish might be saying something else.

Please, I am not throwing out the theory of hybrid vigor. But just stop and think about the price of hybrid vigor. You also ask "But can we really expect to maintain this with continued backcrossing?" I don't know if you can, but I do (and have been doing it for years.)

PART XII OUTCROSSING

Let's look at two words: "outcrossing" and "outbreeding." You have all read authors who say that outcrossing is absolutely no good, and yet these same authors say that outbreeding produces very fine guppies. Outcrossing and outbreeding are exactly the same thing. Look at the definitions: Outcrossing - a cross between strains. Outbreeding - a cross made outside a breed or variety. Are these different? I don't think so and neither do research geneticists.

To make an outcross we select a pair of fish which we think are not closely related. That is the two fish must never be as closely related as those in any form of linebreeding. The best method is to outcross between two different strains of your own fish which you know are not closely related.

There are generally three results from an outcross.

The **FIRST** result is that one which the genetic mismatch is so poor as to prevent fertilization. With no young resulting, nothing more need be said about such a cross.

The **SECOND** result is that one which the young show a wide range in color and shape. There will be a varying number of young which can be grouped together as looking similar. One of these groups will usually resemble the father's strain, while another the mother's strain. The remaining groups and/or individuals will display great variation.

The **THIRD** result, which can only be obtained by outcrossing of **ABSOLUTELY PERFECTLY ESTABLISHED STRAINS**, is that one in which all the young look alike. However, they look totally different than either parental strain. These guppies are generally superb looking, large, fine fish. This third result is that effect called **HETEROSIS**, commonly called "Hybrid Vigor." The term "heterosis" tells the story, in that the fish are almost totally heterozygous. These fish are usually sterile, and represent total genetic scrambling. Because of requiring absolutely perfectly established strains, results #3 are only rarely seen. My tests have given heterosis only 16 times out of 51 outcrosses.

The second result being the most common condition found, let me give the data on an outcross I have made several times. The strains involved were a **Blue Delta** and a **Blue-green Cobra**.

TEST OUTCROSS #1. Male cobra, female blue delta. Young at nine months. The females had some color in their tails but were not outstanding. The males, on the other hand were a sight to behold. They were all Cobras, marked with simple to complex chiming. Tail colors ran from single color solid field to, extremely complex splashes of all colors. Six percent were good deltas, half reds and half blue to blue-green. Fifteen percent were good veils, extremely multicolored with red-orange predominating. Twenty percent were fair veils in all colors. Thirty-five percent were poor veils in all color combinations. The remainder,

although fantastically colored, most would consider junk fish. Oh! It hurts to use that word!! It is interesting to see colors in the young which were not visible in either parent, and some breeders still don't believe in genetics!!!

TEST OUTCROSS #2. Male Blue Delta, female Cobra. Young at nine months. The females were about the same as in test outcross #1. The males were fantastic, and the percentages of tail shapes and color variations were very similar to the males in test outcross #1. The only obvious difference being that none of these had Cobra markings. This test outcross set #1 and #2, displayed an unusual similarity in the young males (except for Cobra markings) which is certainly the exception rather than the rule. Outcrosses should be made in both directions when possible, as you cannot predict which combination will produce the best fish.

"Best fish", this is the problem. We find outcrossing being used in two ways. Outcrossing is a wonderful genetic tool, which can yield fine results. Outcrossing can also be used as a means to an end.

First - outcrossing can be used to introduce a new trait into one of your existing strains similar to our work with the Zebrinus-bronze.

Second - Outcrossing can be used to produce spectacular fish for shows. I realize that the show aspect of the guppy hobby is an extremely important and that it is only through shows that we can see what other breeders are doing.

I know several breeders that do nothing but outcross strains to obtain that best show fish. They simply try a number of outcrosses until they find that particular combination which gives them show fish. It is then only necessary to keep the parental strains going separately until the appropriate time. Then an outcross is made, allowing several months for the young males to mature for the show. The females are never reared. If I had stopped at this point, it might not bother me so much. However, these same outcrossed males are sold through store and possibly at shows. These fish are sold because they often bring a very high price. I dwell on this showing of fish so I can make the following statement. Just because a fish has won the highest honors in a show does not mean that he should be automatically selected as the most desirable fish for breeding. When one is purchasing breeding stock, keep in mind the old warning "CAVEAT EMPTOR" (Let the buyer beware.)

There are many reasons for purchasing a fine guppy, but I will list only three:

1. **You like the fish and want to enjoy his beauty in your tank.** This is an excellent reason for purchasing, as a fine guppy can be very beautiful and should be enjoyed.
2. **You see some trait that you want to add into one of your strains.** This is a valid reason, but be careful, is he sterile? Are his traits worth the price? Remember, as I said before, "many outcrossed fish are sold at high prices simply because they **LOOK GOOD AND HAVE BEEN SHOW WINNING FISH**." Before purchasing, how do you find if the fish is sterile? How do you find if he is a heterosis fish? Don't ask the breeder unless you know him personally very well. I have found very few that seem to know what you are talking about, or will ever discuss it. Many simply say (That fabulous fish must be considered a gamble, a gamble only you can evaluate.)
3. **You want a tank full of guppies that look exactly like that male so you can win some shows like he has done.** This is the greatest dream of the guppy hobby. The establishment of his exact type is very difficult. It can be done, don't forget it, but it takes a long time and a lot of diligent, careful work.

THE TRUTH ABOUT GUPPIES (OUTCROSSING, ADDING RECESSIVES, LINE-BREEDING)

by Tony Abela of Brooklyn Aquarium Society

Any guppy nut with poorer guppies than he would prefer, will always come up with the comment on the drop of a hat that "His stock needs new blood," or in other words, a couple of new fish to add into his own would like to cure things very nicely. On which comment, a lot of misrepresentation can, and often does happen.

For the sake of the subject at hand, let's say you just happen to be one of the people as stated in paragraph one, and you wish to obtain some "new" quality guppies, for the purpose of breeding with your own. If you follow the general trend, all you actually wish is some new guppies that (1) look better than your own and are approximately the same color, and (2) these are within your means financially and otherwise. I think that past experience will show that the average guppy hobbyist assumes that once he can fulfill the above two needs, from then on, he will have it "made."

To which statement I can safely say that this assumption is one heck of a poor way to proceed, except for the occasional individual who has more luck than is good for him.

Like most everything that gives no return for the money, any new blood that is added to existing guppies now on hand, a little advance planning and thought will be well worth the time and trouble taken. The old-time way of breeding guppies "by guess and by-golly" may still be used by those that have no better information to go on, but the modern methods of guppy breeding still makes the best sense and gives the highest rewards.

It is only natural to want a new guppy male that is highly colored, with a wide, triangular-shaped tail, and think this is the exact kind to add into your own fish. However, without some sort of background information on the parentage of the fish, it will be some months before you can know for sure what you actually have. At best, if the guppy is totally unknown to you, the chances are 50:50 that you will even be able to get young (by use of your own females) from such a mating. Chances are even more slim that any resulting young will be an improvement to what you would normally have. It all narrows down to the fact that the truth about guppies, is that seldom do they breed as you wish, or can reliably forecast. With unknown stock, and with doubtful genetic backgrounds, is observing the offspring when and if these appear.

Perhaps a few personal examples, all true, will better put across what I am trying to say.

I was sent some excellent appearing blue delta guppies one time. The breeder who furnished these was best known for these blues and I took some persuasion to get of them. On arrival they did look good, but somehow I had the feeling the fish were not as they appeared. So I did not attempt to blend them into my own blue stock. (I am really not wrong on blue guppies anyway. It took two generations of the strain to show up the discrepancy. They were heavily mixed with pale red guppies. In other words, I heard the, then outcrossed with reds at intervals to maintain the proper shade of blue. A person buying these fish, and using them to add new blood to his own pure blues, would likely end up with the most mixed up combination of colors to where he would be worse off than he was when he started.

Just recently, two members exchanged guppies of a particular color. The less experienced of the two noted that the second generation of the fish he had gotten were all appearing with ragged tails. He immediately

thought of disease, such as tail rot or vitamin deficiency, or something similar. However, he did inquire to the other person in the trade who admitted the fish were originally from a strain of swordtail guppies not too far removed. This then was the apparent tendency of the young to revert towards the more dominant swordtail trait. A not uncommon occurrence BUT one that can be misleading if not known about. Let me take this trend one step further.

Some years back, when triangular tails were first appearing in small percentages of the more common velvet guppies, someone noted that the strains that showed up with the best triangular tails always seemed to show very few male fish with some type of swordtail. Of course, like so many things are, this was laughed off, joked about, and discounted as pure coincidence. Only a few breeders kept quiet, watched and witnessed the proof that delta possesses the genes for swordtails.

The coloring of gold guppies is recessive to the more normal grey body coloring of guppies. This simply means that the gold color will not appear in the resulting young guppies from such a cross. But, if one takes a male and female from these same mixed breed fish, mate them together, then you will get gold-colored guppies. The amount of these has been well worked out by laws of heredity, and it follows closely to these laws. (If one takes the time to save, count, and classify the baby guppies: 25% golds, 75% grey guppies second generation). Any reliable proof on guppy breeding, or genetic volume will give you this information so I won't bother to repeat the same facts. To be brief, the percentages of golden young obtained by breeding brother guppies to sister guppies will gradually increase with the amount of inbreeding if you have the desire to make a strain of true-breeding gold guppies.

By this time I can just hear the reader's complaints, "What will I gain by outcrossing to gold guppies?" So taking it a logical step at a time, here is what one can reasonably expect to get, provided such is wanted.

Hybridizing, in it's full meaning, is the act of crossbreeding two unrelated species to produce "hybrids" (The mating of a female horse to a male donkey, with the end product being a mule-hybrid is one such example). Regrettably, no real (or accurate) hybridizing of guppies has ever been done to my knowledge with this meaning a cross to some other type of fish. However, the generalized term of making hybrids is commonly used with fancy guppies in meaning to cross two strains of guppies that are not related to one another (but are still guppies). To get maximum effects from such a cross in terms of vigorous increased body size, variation in coloring, or to "cure" partial sterility, it is best to use two guppy types that are as far removed from one another as possible, yet will make a compatible mating. (Note: In using the term compatible, it simply means that the end results of the mating will give the wanted results. Such "hybrid" crosses are often ones that give inferior results, or incompatible ones). By use of golden guppies, the two kinds of guppies are removed from one another, genetically speaking as possible with all no guppies being further removed. Therefore, a cross of normal guppy grey guppy strain to a normal gold strain, will at the very least, point of give maximum hybrid progress. This effect will appear immediately evident in the baby fish as they will appear larger and usually more active.

The mixing of gold and grey guppies has more far-reaching effects than the more immediate ones as stated above. However, it is only fair to mention that it does take some time (as measured in generations of guppies from the mixture) to see the more effective results. I am sorry to say that I cannot give reasons to why these effects happen, or even give plausible theories. I have just noted that they do.

Intensifying of color. Breeders may carry guppies in somewhat acid water, or water that may lack certain minerals (but yet be fairly hard), will often complain about guppy coloration going "off" into other shades. Red, for example, going into pink, or orange shades. Half blacks, or 3/4 blacks with red tails, often

become lighter blue rather than the wanted dusky black, (or a charcoal gray). Green fish may fade out to a whitish blue, blue guppies into a mixture of pale blue with other clear areas in the color or into yellow. Other colors not specifically mentioned may become blotched, or a dull, rather than intense coloration regardless of the changes, they are not those wanted. While mixing in a bit of gold guppy may not be a cure all for these ailments, it certainly will help if enough generations of fish are carefully kept and cultivated. Generally speaking, only one grey-gold cross will be needed for the effects to accumulate. It would seem that while the golden genes are recessive to most of those normally associated with grey guppies, eventually, with controlled breeding they become semi-dominant and therefore, the full effects to show does take time.

VIGOR: Most any guppy breeder knows that with continued breeding of any color of fancy guppy, the fish is apt to become smaller, less active, possibly semi-sterile and often, with a loss in body size. An outcross to a related strain is the answer most often given to cure these ills, but if this outcross is to a strain of related golds, the effects will be more spectacular longer lasting, and less apt to adversely effect the coloration. One personal example that I have been carefully watching is a red strain that I got in a trade. At the time of trading, I knew almost nothing about it, had no idea the line carried golds and knew only vaguely of the strain's origin. Twelve generations later, with close inbreeding, a good percentage of golds appears regularly, but even more important, the red coloration is excellent, far richer and deeper in color than expected and it is one of the most active strains of guppies that I have.

COLOR CLARITY: To most guppy people who are active show participants, purity of color comes very close to the top in wanted characteristics. In the past two years, most breeder-entrants have been specializing in improving color and this has brought up some new theories. From my own personal observations, all colors of guppies I keep on hand have been seen to hold color better, hold it longer, and be purer in the one single color in the caudal and dorsal. If they have some gold genes in the line. Assuming that my own experiences are not unique, I suppose this same factor would help others.

BREEDING TIPS: As suggested before, one good reason for most guppy people not taking more advantage of outcrossing, is the lack of good and reliable breeding-type guppies to use. In the case of golden guppies, these are even more scarce. Guppies from commercial sources are often disappointing those bought at show auctions seldom good for breeding purposes, and I regret to say, guppy people needing new stock for mixing show-fish, are extremely suspicious of strangers. Therefore, with the quality of strange guppies one is likely to obtain, outcrosses are seldom what they could be. This is still no reason why they cannot be made to work...all it takes is more patience. Rather than seeing success in the first young fish from such a cross, it maybe far better in the long run to keep the fish, watch them closely, then the best results may appear in the second or later generations. This information I have mentioned a few times before but it certainly bears repeating. Success with guppies does not come over-night, or even in a year except in cases of extreme luck, or a lot of skill.

If you as a breeder, desire to add in a little gold stock to your own, I suggest you watch local pet shops. Florida fish farms sell a lot of gold guppies, but seldom are these likely to look good, or be in the same category as show stock. These still can be useful to use as outcrosses as they usually are quite true-breeding for what they show.

One attribute about gold guppies that may not be fully realized. A gold guppy crossed to another gold guppy will give all golds. It does not matter how many times this same gold has been blended with grey guppies, he (or she), will still be true breeding for one thing...the gold coloration. Naturally, this can be mixed in to the caudal, or dorsal colors, or even with portions of the body being colored, but the background or body color will still be gold. The "gold" by the way, comes in a variety of shades ranging from

near white (sometimes called blonde) to all shades of gold from pale gold to a deep, butter-yellow. In some strains, a litter of baby fish may show all color variations as described, but it takes a sharp (and possibly experienced one with golds alone) to see the differences, especially in the baby guppies.

One of gray guppies (red as one example I am familiar with) once crossed with golds will most always throw percentages of golds from then on, with these becoming more an evidence with close inbreeding. Generally speaking, the addition of coloring over the basic gold will be a variable but if at all possible, use red-golds for use with red-grey guppies, green-golds with green-grey guppies, etc. Naturally, if you can obtain a gold guppy of one color, this is better than none at all and eventually, can be made into another color with the body gold.

The best practice with outcrossing is to keep a strain pure-bred (but is found by actual experience) to be compatible with your own. If tank space is at a premium, a single tank set up to just keep on hand some of the strain needed will be adequate. Even better, as stated many times before, is to find another breeder (or set one up) with guppies related to your own and swap fish at intervals. This can be made into a series of "Linebreeding" methods, or just a way to allow someone else to work strains compatible to your own if they can be kept reasonably pure-bred.

Reprinted from OF FINS AND THINGS, May, 1973

GUPPY GENETICS

PART I - INTRODUCTORY TERMS

by Jack Rosenquisten, PPGA

To acquaint you with heredity and perhaps to further stimulate your interest, I've decided to write a series to try to explain genetics as it relates to guppies. Since the books I read did not mention guppies, or even fish, I had to use my own judgement in selecting characteristics which might apply to guppies. Therefore, any comments about guppies are entirely my own opinion or those of others that I respect. The literature deals almost entirely with the fruit fly and humans, citing other animals to illustrate particular characteristics so that I may likewise be forced to go to these same examples.

Part I deals mainly with the basic definitions which I hope will not be too repetitious for most of you, but they will assure that the following articles may be understood. Some of the definitions will require extensive examples so they will be left to future articles.

Now for some very basic definitions:

GENE: To the breeder this is the smallest unit of inheritance although the geneticist now subdivides this to attempt to explain why genes are different and how they function. We will adhere strictly to what is useful to the breeder.

CHROMOSOMES: All genes are located on threadlike bodies called chromosomes. These are normally found in pairs. The nucleus of every cell contains a set of chromosomes. The fruit fly has eight

chromosomes, while humans and guppies have 46 chromosomes (are we related?). It is estimated that humans have as many as 300,000 genes, so guppies probably have a comparable number. If that seems like a lot, remember that every physical characteristic is determined by at least one gene.

ALLELES: Genes which occupy a specific location on a chromosome usually control a specific trait. Variations of this gene are called alleles, and they can cause corresponding variations in the trait. Since the chromosomes come in pairs, the genes will likewise come in pairs and whether they are both the same or different is really the backbone of heredity.

POLYGENES: Frequently a characteristic is influenced by more than one pair of genes. This group of genes are known as polygenes or multiple genes. Obviously breeding gets more complicated when polygenes are involved.

GENOTYPE: This is the description of the genetic makeup of an organism usually described symbolically with letters.

PHENOTYPE: This is the appearance of the organism caused by the genetic makeup. Indiv. Juvs with different genotypes may still have the same phenotype, or appear to be the same.

HOMOZYGOUS and HETEROZYGOUS: As mentioned earlier, genes usually come in pairs. If both genes of the pair are the same, the organism is said to be homozygous. If both genes are different, the organism is known as heterozygous.

DOMINANT or RECESSIVE: The relative importance of each allele is classified as dominant or recessive to each other allele. Possession of one dominant allele is sufficient to establish the dominant phenotype. The heterozygous organism will look identical to the organism that is homozygous for the dominant gene. Both identical recessive genes are needed to express the recessive phenotype, unless, of course, the odd gene is a third allele that is even more recessive. There can also be an intermediate expression where the heterozygous organism is a different phenotype than either of the homozygous genotypes (in other words, three different appearances result from the various combinations of two different genes). Geneticists use capital letters to denote dominant genes and small letters to symbolize recessive genes, i.e. genotypes for brown eyes could therefore be written as BB, Bb or bb where B is a dominant gene for brown eyes and b is a gene for a recessive trait that is not brown eyes. Multiple alleles are written as letters with various superscripts.

NOW THAT YOU KNOW THE BASICS LET'S PROGRESS INTO HOW THESE TRAITS ARE PASSED ON TO THE OFFSPRING.

MEIOSIS: This is the process by which cells with a normal number of chromosomes divide to form the sex cells (eggs or sperms) necessary for fertilization. This division separates each chromosomal pair so that each sex cell has only half the normal number of chromosomes. When they join during fertilization, the number of chromosomes will again be correct. It is a pure game of chance as to which of each chromosomal pair is in each egg or sperm, but all of the genes on each chromosome will move as a unit (with some exceptions).

SEX DETERMINATION: As mentioned earlier, chromosomes occur in pairs. Excluding abnormal cells, these pairs are usually matched in size and approximate appearance. The normal exception to this rule are the pair of chromosomes that determine sex. In humans, fruit flies and guppies, the male has a pair of chromosomes differing greatly in size. The smaller of the pair is designated as the Y-chromosome and the larger is designated as the X-chromosome. The female, in contrast, has a pair of X-chromosomes. These chromosomes are inherited the same as all the others so that an individual with an XY chromosome pair is male and one with XX chromosome is a female.

SEX-LINKED GENES: Genes located exclusively on the X-chromosome are called sex-linked genes since their inheritance is related to sex determination. In the hobby this is usually referred to as **X-linked** and I'll stick with that usage. A good sample of the characteristic are some of the half-black strains of guppy.

HOLANDRIC GENES: This term applies to genes located exclusively on the Y-chromosome or **Y-linked**. Few genes appear to be located on the chromosome so that this condition is relatively rare. Examples of this in guppies are also certain half-black strains, snake skins and also the tangential-eye-line.

AUTOSOMAL GENES: This covers all genes located on the other chromosomes. Their pattern of transmission is therefore independent of sex determination.

INCOMPLETELY SEX-LINKED GENES: Genes in this category have alleles on both the X and Y chromosomes so that they behave like autosomal genes but their pattern of transmission shows their relation to sex determination. I don't know of any guppies that fit this pattern but certainly the half-black strains mentioned above are candidates. If they are indeed alleles, I think some of the swordtail guppies are also possible candidates but I'm now convinced that the double-swords that I have are caused by a dominant autosomal gene. It should be obvious that outcrosses of this type of gene with other strains will cause some confusing results.

SEX-LIMITED GENES: These are genes which maybe present in either sex but are expressed in only one sex. Certainly this must apply to the color and other secondary sexual characteristics of the male guppy. Female guppies treated with male hormones will color like the males and start to acquire male characteristics proving that the females have the genes to make this possible. Hormone treated females can even develop a gonopodium (male anal fin) although they will never be fertile males. In the fruit fly on y the genes for male fertility are located on the Y-chromosome and this appears to be the case with guppies.

SEX-INFLUENCED GENES: The class consists of genes which are dominant in one sex can be recessive in the other sex. The best example I can think of concerns the X-linked hemophilia gene in humans. In men only one gene is necessary (only one is possible) to cause hemophilia while a woman is an unaffected "carrier" of the gene. In contrast, a woman with two genes for hemophilia is herself a hemophiliac.

LINKED GENES: This term covers genes which govern different characteristics but are located on the same chromosome so that they are inherited together. Of course this is a great nuisance to a breeder who is trying to separate an undesirable trait from a desirable trait. I would guess that the small dorkies associated with snakeskins are an example of linked genes. The next two terms, however, offer some hope for the frustrated breeder. It should be pointed out that if linked genes govern the same trait the breeder will be obvious of the fact and assume that there is only one gene involved.

CROSSOVER: An entirely unpredictable phenomenon which occurs as part of crossover where linked genes are indeed separated. Somewhere in the formation of the gametes (a general term for eggs and sperms) a pair of chromosomes break and exchange halves. If the above example is true, someday a breeder maybe lucky enough to have a large dorsal gene on one chromosome and a snakeskin pattern on its companion when a crossover occurs. Since snakeskin is a Y-linked gene (although some claim there are also X-linked snakeskins) this would be a most unusual crossover and could result in sterile males if too much of the Y-chromosome is lost. Hopefully if this fish turns up it will not be cued for some other reason before the crossover is noted.

MUTATION. In the strictest sense, this is the occurrence of a gene which was not inherited. It may be a gene that was altered with chemicals, radiation, heat or by accident. Whatever the reason, a new trait may show up and if desirable could lead to a whole new strain of guppies. The breeder, of course, will probably call anything that wasn't expected, a mutation, even though it may only be a recessive trait that has finally surfaced.

EPISTASIS AND MODIFIERS: These two conditions probably should not be lumped together, but on a basic level these genes alter or inhibit what other genes do. Thus, there are autosomal modifiers of the half-black genes which make the "black" even more black. Sometimes one pair of genes within a polygene inhibits the function of the polygene. This condition is known as epistasis. An example of epistasis is the gene for albism which inhibits the genes for pigmentation.

PART II - MONOHYBRID CROSS

The simplest genetic case is that of the monohybrid cross. This involves one pair of genes which determine a particular physical characteristic, such as body color. Where variations (alleles) of this gene exist the appearance (phenotype) of the organism will depend upon which alleles are present (genotype) and their relative importance (dominant or recessive).

A good example of a monohybrid cross (meaning, in this, of a cross between guppies showing a bronze body color and the wild gray body color. Body color is the background color of the body scene which in many of the males is mostly covered by a color pattern but always shows around the male's head. Body color is much easier to observe in the female guppies since, with the exception of the half blacks, most of the females do not have color patterns on the body. Body colors are autosomal traits which is to say that they are not caused by genes located on the X or Y chromosomes. Bronze body color is characterized by a gold body showing appearance. Gray body color is the body color of most guppies and is the color of the wild guppies. Other guppy colors are silver, gold, blond, cream and blue.

Bronze body color is a recessive allele of the dominant gray body color so that a bronze guppy is a homozygous genotype (both genes the same). The genotype is symbolically written as bb. Note that two letters are used to denote that a pair of genes is involved. Note also that lower case letters are used to indicate that the genes are recessive alleles.

Gray body color is a dominant allele so that a guppy which is phenotypically gray may be either a homozygous or heterozygous genotype. The genotypes respectively, are symbolically noted as BB and Bb. B is the notation for the dominant gray gene rather than G in order to relate the alleles by a common letter. If different letters were used it would become difficult to distinguish alleles in multiple gene discussions. The accepted practice is to derive the symbol from the recessive gene.

Now for an example of what all this means to the breeder. Let's suppose that you go to one of our fine guppy shows and purchase at the auction a beautiful male (or female, bronze guppy. On the way home you are filled with visions of founding a dynasty of bronze guppies. Upon arrival at home you discover your first problem - all you own are gray guppies. What to do?

Aside from the obvious that you should have purchased a pair of bronze guppies, the only recourse is to mate him to one of your gray guppies. When the babies arrive you discover your second problem - all the

babies are gray. Have you lost the bronze color? Not at all. This is just a simple case of the gray being dominant and even though all the babies look gray, they are all carrying a bronze gene.

Before proceeding further, let's diagram the above. Remember that normal body cells have pairs of genes carried on pairs of chromosomes (known as the diploid number). During the formation (meiosis) of the gametes (eggs and sperms) these pairs are divided and each gamete receives only one (the haploid number) of the pair. With the union of the egg and sperm during fertilization the diploid number is again present. Each parent therefore contributes half of the babies' genes. The gray gamete is then noted as B and the bronze gamete as b. Of course, if you are dealing with pure genotypes all of each parent's gametes will be the same. A series of squares is used to illustrate the possible combinations of the gametes.

Figure 1 is drawn for the above case. The top row shows the possible male gametes (in this case they are the same). The left column shows the possible female gametes (again the same). The squares contain the combinations within the fertilized cells. All the resulting genotypes are Bb which is the gray phenotype.

	b	b	
B	Bb	Bb	B — dominant gray gene b — recessive bronze gene Bb — gray phenotype
B	Bb	Bb	

Figure 1 - The P-1 Outcross

The parents are called the P-1 generation and the babies are called the F-1 or first filial generation. Now what does all this have to do with your bronze dynasty? It is obvious from the above that you can breed that bronze with every gray you own and never see another bronze so that your next step will have to be different.

You now have three types to work with, namely the grays, the lone bronze, and the hybrid F-1. Of course, using the pure grays will be of no help in establishing a bronze line so that leaves two choices. Looking ahead you can see that a cross between fish that both carry bronze genes will yield some bronze babies but is there an important difference between the two choices?

Let's look first at a sibling (brother-sister) cross of the F-1 the babies are the F-2 generation and subsequent descending sibling crosses would result in F-3, F-4, etc. Figure 2 shows the squares for this case. The gametes are now different since the F-1 are hybrids. Assuming equal numbers of the gamete types and equal survival of the young (not always true), each of the four squares represent the genotypes of one-fourth of the young.

	B	b	
B	BB	Bb	Bb — gray phenotype bb — bronze phenotype
b	Bb	bb	

Figure 2 - The F-1 Sibling Cross

This means that among 32 fry you can expect to find four male bronze and find four female bronze babies. Is this the best you can do? If that bronze male is no longer alive, the answer is yes. If he is alive, let's examine a backcross between the F-1 and the bronze P-1. Incidentally, there is no good designation for the resulting fry. One book used R-1 for the resulting generation, but this does not distinguish between

the two possible backcrosses nor subsequent possible backcrosses. Most references last call it a "new" P-1 or omit using symbolic designations.

Figure 3 illustrates a backcross between the F-1 and the bronze P-1. The bronze gametes are in the top row and the hybrid gametes are in the left column.

	b	b	
B	Bb	Bb	Bb — Gray phenotype
b	bb	bb	bb — Bronze phenotype

Figure 3 - F-1 x P-1 (Backcross)

As you can see, two-fourths or half of the fry are now bronze so that the backcross doubles the number of bronze fish and this is certainly the best of the two choices.

There is however a much more important difference between these two crosses if you want to produce as many bronze as quickly as possible.

Let's look at the F-2 in Figure 2. The ratio of gray to bronze phenotype is 3:1 (the famous Mendelian ratio). The genotypes of BB, Bb and bb however, are in the ratio of 1:2:1, respectively. What this means is that if you choose any of the gray for breeding, you have a one in three chance of selecting one that does not carry a bronze gene. Crosses between F-2 grays are the equivalent of one of the following: (1) the F-1 cross, (2) a backcross of F-1 to the P-1 gray, or (3) a cross between two pure grays. Crosses between the F-2 bronze and F-2 gray is the equivalent of either: (1) the backcross of the F-1 to the P-1 bronze or (2, the original P-1 cross. The reason for the multiple choice is that the results cannot be predicted since the gray phenotypes are indistinguishable. As you can see, using the F-2 gray fry may not produce additional bronze fry and may even eliminate the bronze gene.

Well what about the fry in Figure 3? The phenotype ratio is 1:1 and it is the same as the genotype ratio. No homozygous grays exist. All crosses between grays are the equivalent of a backcross of the F-1 and bronze P-1. Therefore, all of the fry are useful for further breeding, avoid however, breeding gray to gray since some pure grays will again be produced.

Of course, if you stuck with having to make an F-1 cross, the best choice for the next step would be to use only F-2 bronze for breeding. If you're not satisfied with them because of other attributes then breed only bronze to gray, preferably a backcross of an F-2 bronze with the F-1 since this will at least assure that all of the grays used are hybrids, and all of the resulting grays will also be hybrids. The F-1 x F-2 bronze backcross is the equivalent of the F-1 x P-1 bronze backcross.

The above illustrations, while true, are not so typical. In most cases the guppy breeder is after male characteristics and although the females carry the characteristic, the females of the homozygous recessive genotype are usually indistinguishable from the females of the homozygous dominant genotype.

The odds of picking the correct female F-2 is then one in four since there is only one female phenotype although there are still three genotypes. That is to say that although there are three different pairs of genes in the various females, they all look alike (of course this is no longer a discussion of body color). The prudent use of the backcross to quickly eliminate all homozygous dominant females becomes necessary. The odds of finding the right female are then reduced to one in two, and success can be measured by the resulting male offspring.

I recall one of our meetings, when one of our members asked when the bronze he had purchased would show up in his breeding program he was up to the F-4 and getting concerned. From the above I think you can deduce what had happened.

Let's try exactly the opposite case now. Suppose you brought home a gray bodied guppy and all the others you owned were bronze. Although this would be an unusual case, the same would hold for any dominant characteristic introduced into a line with a corresponding recessive characteristic.

Figure #1 represents the P-1 outcross since in both cases the first outcross is a bronze to a gray. The F-1 as before are all gray. Mission accomplished? Not exactly. As long as you breed gray to gray the fry will be at least three-fourths gray, but on occasion an unwanted one-fourth will be bronze. The method most breeders would use in this situation would be to just keep culling the unwanted fry and their parents which have just proved that they are carrying the unwanted gene. Eventually culling will be successful.

There is a more organized way, however, of eliminating the recessive gene. It's more complicated and whether you'll want to take the trouble will depend upon how badly you want to remove the unwanted recessive gene. The method is called a "test cross".

In a test cross a guppy is tested for a hidden recessive gene by deliberately crossing it to a guppy that displays the recessive gene. If any of the fry display the recessive gene, it means that both parents contributed a recessive gene so that the parent in question is indeed carrying the recessive gene.

The test cross works fine if you want to test a male guppy as long as you make sure the recessive female is a virgin. Testing a female that is to be used for breeding is an entirely different case. Once a female has mated she can carry the sperm for months and is therefore considered contaminated for further breeding purposes. The method then is to test only the males unless you are willing to test cross a large number of sisters of the intended breeder female to be reasonably certain of the virginity of the female.

Note that a backcross of the F-1 to the P-1 gray, which is always a good idea, is of no apparent help since all the fry will be gray, half will be genotype BB and half will be genotype Bb. This will be better than the F-1 sibling cross (see figure 2) since, in addition to one-fourth bronze, only one-third of the grays will be genotype Bb.

PART III - SEX-LINKED GENES

In Part I it was mentioned that male guppies have a distinct pair (or non-pair) of chromosomes designated as the X and Y chromosomes, respectively while the females have a pair of X chromosomes. In Part II, inheritance of autosomal genes (genes on the other chromosomes) was explained with the presumption that the same results could be achieved regardless of which of the strains of an outcross contributed the males and females. The immediate consequence of sex-linked genes is that it is very important which strains contribute the males and females.

When I mention sex-linked genes the broadest common usage is implied, namely genes located on either the X or Y chromosome. Genes located exclusively on the Y chromosome are actually known as holandric genes. To avoid confusion I will use the more graphic terms of X-linked and Y-linked genes. The inheritance of sex-linked genes can be illustrated with the same system of squares used in Part II. The letters for the gametes now represent chromosomes instead of genes but, with the exception of crossovers

chromosomal Breakage), these are equivalent since all the genes on a chromosome move as a unit. **Figure 1** illustrates the expected offspring which, as might be expected, are 50% males and 50% females. (Other factors can change the gamete ratios in some strains.)

		Male		
		X	Y	
Female	X	XX	XY	XX — Female
	X	XX	XY	XY — Male

Figure 1 - Sex Inheritance

Although the above may seem obvious, a careful examination produces some important rules, namely:

1. Only males can have a Y-linked gene.
2. Males can have only one X-linked gene.
3. Females have two X-linked genes.

Sex-linked genes fall into three broad categories which determine how their effects will be displayed. They are:

1. Y-linked without any X-linked allele. This can be called **exclusively Y-linked**.
2. X-linked without any Y-linked allele. This can be called **exclusively X-linked**.
3. **Incompletely sex-linked** meaning that an X-linked gene is an allele of a Y-linked gene.

First, let's deal with exclusively Y-linked genes. None of the texts illustrated inheritance of sex-linked genes so that **Figure 2** is my own contrivance to illustrate this case. This figure is a mixture of chromosomes and a gene, but again, I see no harm since they normally act as indivisible units. The gametes are now X for the X-chromosome and YT for the Y-chromosome with the linked gene named T. The T stands for the tangential-eye-line (TEL) gene which is a Y-linked gene. The TEL gene is exhibited in males as a line that starts at the eye and runs horizontally to just forward of the dorsal. I first saw this term used on these pages by Dr. Larr and recognized it as what I called the eye-stripe.

		Male		
		X	YT	
Female	X	XX	XYT	XX — Female
	X	XX	XYT	XYT — Male with tangential-eye-line

Figure 2 - Exclusively Y-linked

Figure 2 could be called the F-1 of an outcross of a TEL male and an unrelated female but the same figure also illustrates the F-2, F-3, etc. In fact, this figure represents the cross of a TEL male with any

female guppy. The results are that 100% of the male fry will exhibit the TEL trait. Incidentally, the use of a capital letter T is not indicative of a dominant gene in this case, since there is no competing allele its presence will always be visible.

How does a breeder distinguish between a Y-linked gene and a dominant autosomal gene? The F-1 males of both crosses are 100% like the father. For the dominant autosomal gene, only 50% of the F-2 males will be like the P-1 male, but the Y-linked F-2 will be 100% like the P-1 male. The most important difference is that the females of the Y-linked strain can in no way introduce this gene into another strain. If you want to introduce the TEL characteristic to a strain, you must use a TEL male. If you need an illustration for an outcross using a female from a TEL strain, then it is **Figure 1**, and if you observe that the T gene is not present, that is the point.

The above discussion holds true for any exclusively Y-linked gene such as some of the half black or snakeskin patterns. The females in these half black strains will, of course, not be half blacks. The half black females that you've seen are caused by X-linked genes. I'm told that there are also X-linked genes.

With exclusively X-linked genes, the effects upon the males and females will be different. Females can carry two X-linked alleles so that if they can exhibit the genes, the traits will be dominant, intermediate or recessive just as with the autosomal genes. The males, however, have only one X-linked gene so that whatever gene is carried will be exhibited unless it is a sex-inhibited or sex-influenced gene or is modified or masked by an autosomal gene.

The X-linked half black pattern is a dominant gene in the female grey bodied guppy. In one strain of gold bodied guppy that I worked with, the X-linked black gene was recessive so that the gold females would show the half black pattern only if it had both genes. **Figure 3** illustrates an outcross between a homozygous half black female and a grey bodied male. The letter g for grey is used in keeping with the convention of letting the recessive trait name the gene.

		Male		
		Xg	Y	
Female	XG	XXGg	XYG	G - X-linked half black gene
	Xg	XXGg	XYG	g - X-linked non-half black grey gene
				XYGg - Half black female
				XYG - Half black male

Figure 3 - P-1 Outcross

The P-1 fry are 100% half black just as with a dominant autosomal gene. Once again the difference can be seen in the results of the F-1 sibling cross shown in **Figure 4** on the next page.

		Male		
		XG	Y	
Female	XG	XXGG	XYG	
	Xg	XXGg	XYg	

G - X-linked half black gene
 g - X-linked non-half black gene
 XYg - Gray male
 XXGG, XXGg - Half black female
 XGY - Half black male

Figure 4 - P-1 Sibling Cross

The F-2 females are 100% half blacks and the males are 50% of blacks and 50% greys. If half black was instead a dominant autosomal trait, both male and female F-2 would be 75% half blacks. As with the autosomal traits, the heterozygous and dominant homozygous females are the same phenotype. Culling these heterozygous females is not as critical as with some autosomal traits because the new half black "strain" can never produce a grey female as long as only half black males are used since the male cannot hide the recessive gene. Even if the heterozygous and homozygous female do not display the male trait, as is the case with the Zebrinus or Cobra (vertical bars in the male) trait, the heterozygous female can be readily identified since one-half of her male babies will not show the trait.

Now let's look at the above example from the standpoint of the recessive X-linked gene. I've avoided referring to an X-linked grey gene because it probably doesn't exist. Most likely the recessive gene has no visible effect on the guppy.

A breeder might acquire a half black male hoping to add size and other attributes to a grey bodied strain but without adding the half black pattern. This outcross is shown in Figure 5.

		Male		
		XG	Y	
Female	Xg	XXGg	XYg	
	XG	XXGG	XYG	

G - X-linked half black gene
 g - X-linked non-half black gene
 XYg - Gray male
 XXGg - Half black female
 XYG - Half black male

Figure 5 - P-1 Outcross

All the F-1 females are half blacks while none of the males are half black. The goal of eliminating the half black pattern is, therefore, easily obtained, but those other desirable traits disappear with the half black. The half black gene is apparently linked with other important genes on the same X-chromosome. Of interest is the fact that the breeder, by using only half black females and grey males from the F-1 and succeeding generations can maintain a strain that throws 50% half black males and 50% grey males as assumed in Figure 6. Maintaining this type of strain greatly increases the chances that a crossover will occur between dissimilar X-chromosomes which could result in a new strain. Many strains which have been crossed in and out with half blacks are now showing the same type of body coloring and could be called half purples, half reds, half blues, etc.

		Male		
		Xg	Y	
Female	XG	XXGg	XYG	
	Xg	XXgg	XYg	

G - X-linked half black gene
 g - X-linked non-half black gene
 XYg - Gray male
 XXGg - Half black female
 XXgg - Gray Female
 XYg - Half black male

Figure 6 - F-1 Sibling Cross

The explanation of incomplete y sex-linked genes is fairly complicated and I don't know of any guppy characteristic that fits this type. Just to show how this would be handled however, Figure 7 illustrates an outcross between a male with an X-linked and Y-linked dominant gene and a female with a recessive X-linked gene.

		Male		
		XG	YG	
Female	Xg	XXGg	XYGg	
	Xg	XXGg	XYGg	

XG — dominant X-linked gene
 Xg — recessive X-linked gene
 YG — dominant y-linked gene

Figure 7 - P-1 Outcross

In this case both males and females will be 100% of the dominant phenotype. Many other combinations are possible in the outcrosses as the gametes from the various guppies could be XG, Xg, YG, or Yg. There are four different male genotypes and three different female genotypes which yields twelve possible crosses. The difference between incompletely sex-linked genes and autosomal genes is that none of the combinations possible for the incompletely sex-linked genes will yield a 75% - 25% ratio as occurs in many autosomal crosses. The male fry may be 100%, 50% or 0% of the dominant phenotype and the females will independently also have one of those proportions. As with the autosomal genes, the recessive trait will only be displayed if both genes for the recessive trait are present.

As you can see determining what kind of genes you're dealing with can be complicated, particularly if your outcrosses don't start with pure strains. Only making careful counts of the fry can this determination be made, and it may take a number of back crosses. So far we've dealt only with a single pair of genes.

PART IV DIHYBRID CROSS

Until now the discussion has concerned the effects of one pair of genes, or a single gene in the case of sex-linked genes. Quite often, however, multiple pairs of genes or polygenes are involved. When two pairs of genes are involved a cross between two different homozygous strains is known as a **dihybrid cross**.

An example of a dihybrid cross is the cross between a gold and a bronze guppy. Although both the gold and bronze body colors are each determined by a single pair of recessive genes, the pairs are non-allelic. It is possible, therefore, for a guppy to possess both pairs of genes. What does a guppy with the combined genes look like? To quote Midge Hill in the IFGA Bulletin:

"In the case of the double recessive of both gold and bronze, the resultant individual has a distinct body color which differs from the gold by being a paler yellow color, melanophores are usually very few in number and are sometimes almost completely absent. **Cream body color is the result of a combination of both bronze and gold when both are in their pure state. There is no gene for cream!**"

Let's look at what it takes to establish a cream line by starting with a single cream guppy. Of course, since we know the genetic makeup of the cream guppy, the best outcross would be into either a gold or bronze line. In order to illustrate the dihybrid cross, however, we'll make an outcross into a grey bodied line. Figure 8 shows this outcross. The notation for a cream guppy is bbgg where b is the recessive bronze

gene and g is the recessive gold gene. The homozygous grey guppy notation is BBGG, where B is the dominant allele of the bronze gene and G is the non-gold dominant allele of the gold gene. The gametes (eggs and sperms) must now be represented by two letters to account for the two pairs of genes. Since the types are homozygous, all the gametes will be the same so that the system of squares can be reduced to a single square. What do the F-1 look like? Since there is neither a pair of gold nor a pair of bronze genes, the F-1 are all grey.

	bg
BG	BbGg

BbGg — grey phenotyp

Figure 1 - Cream x Grey Outcross

Just as with the monohybrid cross, the next choice is either an F-1 sibling cross or a backcross of the F-1 to the cream parent. Figure 2 shows the sibling cross using a system of squares, only now there must be 16 squares to account for the fact that each parent can contribute four different gametes (2 alleles for the gold gene multiplied by 2 alleles for the bronze gene).

	BG	Bg	bG	bg	
BG	BBGG	BBGg	BbGG	BbGg	b - bronze gene B - non-bronze gene g - gold gene G - non-gold gene BBGG, BBGg, BbGg - grey phenotype BBgg, Bbgg - gold phenotype bbGG, bbGg - bronze phenotype bbgg - cream phenotype
Bg	BBGg	BBgg	BbGg	Bbgg	
bG	BbGG	BbGg	bbGG	bbGg	
bg	BbGg	Bbgg	bbGg	bbgg	

Figure 2 F-1 Sibling Cross (Combination of Gametes)

As in the previous cases the contents of each square is the combination of the column and row headings (gametes). To preserve order the letters are written in alphabetic order with capital letters preceding small letters. Each of the 16 squares represents an equal proportion of the fry. A careful count using the legend of Figure 2 shows the phenotypes in the following ratio:

9 grey: 3 bronze: 3 gold: 1 cream

This is the ratio where each pair of recessive genes affects the phenotype. Sometimes each recessive pair does not affect the phenotype. The ratios will then show various combinations of the above numbers such as 15: 9: 7, 2: 3: 1 or 9: 4: 3.

As can be seen, the use of squares as in Figure 2 can be cumbersome. There are several simpler methods, one of which is shown in Figure 3. The top row represents the genotypes obtained when only one pair of genes is followed using the squares. The left column represents the genotypes of the second pair of genes. The numbers in parentheses are the phenotype ratios. As before, the letters in the squares represent the combinations of the column and row headings, but the numbers are omitted. Only as many columns and rows as are necessary are used.

	(1)GG	(2)Gg	(1)gg	
(1)BB	(1)BBGG	(2)BBGg	(1)BBgg	Phenotypes GG, Gg — grey gg — gold BB, Bb — grey bb — bronze Combination same as Fig. 2
(2)Bb	(2)BbGG	(4)BbGg	(2)Bbgg	
(1)bb	(1)bbGG	(2)bbGg	(1)bbgg	

Figure 3 - F-1 Sibling Cross
Combining the Genotypes of Each Pair of Genes

The breeder's problem in trying to establish a cream line by outcrossing to a grey line is considerably more difficult than working with only one pair of genes. The above ratios indicate that in the F-2 only 1/16 will be cream. This means that in 32 fry, on the average, only one male and one female cream guppy will occur. Since averages are seldom realized, there may not even be any cream guppies in this small sample.

With the monohybrid cross, the backcross of the F-1 to the recessive P-1 was better than the F-1 sibling cross. Will this hold true for the dihybrid cross? Figure 4 illustrates this case, which genetically is bbgg x BbGg, using the method of Figure 3. The row and column headings turn out to be the genotypes of a backcross for a single pair of genes. The parentheses numbers are not shown as they are all one (1).

	Bb	bb	
Gg	BbGg	bbGg	Phenotypes per Figures 2 and 3
gg	Bbgg	bbgg	

Figure 4 - F-1 x P-1 Backcross

As can be seen, the ratio of phenotypes is now— 1 grey: 1 bronze: 1 gold: 1 cream.

The backcross, therefore, yields four times as many cream guppies for the same number of fry. The F-1 x F-2 cream will also yield the same proportions. Just as with the monohybrid cross the grey F-2 should be avoided since using them could lead away from the goal of a cream line.

The genotype ratios of the above examples apply to any dihybrid cross. As mentioned earlier, the phenotype ratios will vary depending on the effect of the genes.

As an example, take the above case, if the bronze and gold body colors could not be expressed but, instead, were just additional greys. The F-2 would then have a phenotype ratio of 15 grey to 1 cream.

If two types of a non-allelic albino were crossed, the F-1 would be grey since a matched pair of albino genes is needed for the fry to be albino. The F-2 will have a phenotype ratio of 9 grey to 7 albino. The F-2 albino consists of 3 of each type of albino and 1 double (both types combined) albino.

In a cross between a gold and an albino, the F-1 are again grey. The F-2 now have the phenotype ratio of 9 grey to 4 albino to 3 gold. One of the four albino is actually a combined gold and albino.

More complex cases where three or more pairs of genes are involved could be described, but there isn't room to outline what can be counted in a litter of guppy grey. With three pairs of recessive genes, only 1/64 of the F-2 outcross to a dominant type will exhibit the recessive phenotype, and, if it is exhibited by only one sex, then only 1/128 will exhibit it. Similarly, with four pairs of recessive genes, only 1/256 of the F-2 will be the recessive genotype. Each pair of genes reduces the chance of a homozygous recessive showing up in the F-2 by a factor of four.

PART V SLIGHTLY MATHEMATICAL

Prior articles have covered many of the genetic ratios encountered while breeding guppies. Although precise ratios were discussed, it must be realized that a careful count of fry, particularly in a small sample, will only be an approximation of these ratios because of both genetic and mathematical considerations.

First let's take a look at the mathematical aspects. When the odds of an event happening are one out of two such as the flip of a coin producing heads, many people are often fooled in attempting to apply the same odds to a large number of similar events. For instance, what are the odds of tossing two coins and getting exactly one head and one tail? You might guess one out of two and you would be correct. There are four possible combinations, two of which fit the requirement.

What about simultaneously tossing four coins? What are the odds of exactly two heads and two tails in the toss? Again you might guess one out of two and this time you would be wrong. There are sixteen possible combinations, only six of which are two heads and two tails. Interesting enough, in eight out of the sixteen combinations there will be three heads and a tail or three tails and a head. Even though these figures were calculated I'm sure some of you are already searching for some coins to check it out. There is nothing wrong. The total number of heads and tails for all combinations combined is still equal.

What does this have to do with guppies? Simply stated this means that in one litter of fry don't be surprised if the number of males and females is not equal. Only if it is consistently repeated is suggestive of anything meaningful. The same holds true for all genetic ratios.

As an example of how the above applies to guppies, in a litter of 30 fry there are more than one billion possible combinations of males and females but only about one-sixth of them are equally divided. About 50% of the time the ratio will be either 16:15 or 15:15. Of course, 30 males could show up, but the odds are a billion to one against it. These are examples of what is known mathematically as the binomial distribution and that's about as far as I'll take it.

Aside from the pure laws of chance there are many genetic factors which may change the expected phenotypic ratios. Many of these factors can be classified as lethal genes. The term implies that possession of a lethal gene or pair of genes is immediately fatal, but the term actually encompasses a much larger field. Some genes, of course do cause embryonic deaths so that the expected birth ratios are not realized. Lethal genes are actually genes that affect viability, survival or propagation of the species. Premature deaths before the fry are classified will cause an erroneous phenotypic ratio to be observed. The gene for yellow coloration is believed to be a lethal gene. Supposedly, if a pure yellow without any black impurities was born it would be short lived.

Just because the term lethal gene was used, don't think that only undesirable genes were meant. In fact, most of what we think of as desirable genes would be lethal genes in the wild. Fish with bright colors attract predators and large fins that hamper swimming will certainly hinder escape. In this regard I get annoyed with those that call albinos cannibals. The fact is that albino babies just are not built for living. The albino parents also pursue their grey (hybrid, of course) offspring, but quickly lose interest when they keep disappearing.

Other lethal genes which can frustrate the breeder are those that cause sterility or inability to mate. One of my less happy experiences was in breeding hi-fin swordtails (X. Hellertii). As the fins got longer

the numbers diminished. It was only after I had lost the strain that I learned that the hi-fin gene is lethal in several respects. The hi-fin gene is a dominant gene. A double dose of this gene causes a premature death. The male's large gonopodium also hinders mating and this strain throws a high percentage of males, mostly males. The best matings were between the lo-fin males and the hi-fin females, but when there were sufficient hi-fin males I culled the lo-fins. End of Line. This serves to point out that to successfully work a strain, you must know all the facts or be lucky.

Environmental factors can also throw off the expected ratios. Some strains are harder than others and and poor conditions will kill off the weaker types before they are classified. Aminos and golds will also be eaten if there are not ample hiding places. Any losses, if known before fry are classified should be counted as an unknown factor and not ignored. Ratios which do not fit the expected ratios should be suspect since they may indicate embryonic deaths. In the swordtail example above, a cross between a hi-fin and a lo-fin would always yield half of each, indicating hi-fins do not possess a pair of hi-fin genes. Sex-linked genes are ruled out since both sexes can be hi-fins. Matings between two hi-fins (if possible) would yield two hi-fins to a lo-fin, instead of the expected three to one since the double hi-fin genotypes die, usually as embryos.

Another factor which often gives unexpected results is a cross between two supposed pure bred animals, but which each actually have some of the genes of a polygene. Consider a characteristic which requires four pairs of recessive genes to be displayed. A strain displaying this characteristic when crossed to a strain not displaying the characteristic would be expected to again show the characteristic in only 25% of the F-2 fry. It is possible, however, that 1/4 of the F-2 fry display the characteristic; the reason being that the other strain already had three of the four genes. The non-displaying strain would hardly be expected to be pure for these three genes since the breeder was unaware of their existence and, thereby, could make no effort to select them. The breeder is then faced with conflicting results depending on whether the non-displaying fish selected has one, two or three of the required genes, and singly or in pairs. Probably the most puzzling example of this is where both strains carry some of the required genes, but neither carries them all. A chance outcross may produce a new characteristic, but the breeder will be hard pressed to capitalize on his find. In this case, remember that backcrosses on both sides are the best bet.

Other factors that can change the phenotype ratios are mutations or errors. A **mutation is the occurrence of a gene which was not inherited**. By definition then, its appearance cannot be predicted on the basis of ancestry. Mutations do not have to be something that has never been seen before. Genes are complex molecules and they can occasionally change their structure to a previously seen form or to a new form. This is one explanation of why some strains will occasionally yield an albino or gold baby instead of a minimum 25% which would indicate an inherited trait.

Crossovers are the breaking of chromosomes and the rejoining of mismatched pieces. In this manner a pair of chromosomes exchange pieces. Genes which were linked on a single chromosome are thereby separated and the observant breeder may be able to have discovered that crossovers are a statistically predictable occurrence. The frequency of occurrence depends on the species. This phenomenon might explain why one of my snakeskin (Y-Lined) males recently fathered a litter in which one of the males was not a snakeskin.

Another phenomenon which can change the results is epistasis. This is where one gene can nullify the effects of another gene. In guppies there is a single pair of recessive genes which cause a darker yellow/gold body color. There is, however, another non-lethal pair of recessive genes which will partially nullify the effects of the first pair so that a dull gold body color results. Similarly, a pair of albino genes will nullify many color types, in addition to masking all body colors.

As you can see, the subject of genetics is far from simple. The main scope of these articles is to inform you what may be occurring so that you can evaluate the results and take appropriate action.

reprinted with revisions from the Guppy Roundtable July 1973

GUPPY GENETICS SOME FACTS AND FALLACIES

By Jim Kerly, Manchester, England

Recently some excellent articles have been written on Genetics, specifically where Guppies are concerned. It is not the intention of this article to teach you Genetics. This subject has been well covered. Rather to stop and sort out some of the "old wives tales" that annually creep into our literature, usually perpetuated by authors that have picked the meat from various treatise and without verifying any of the facts blindly repeat them.

Let us begin by looking at **TELEGONY** or "infection of the germ". Followers of this belief hold the view that the first male to which a female guppy is mated has an influence upon her subsequent broods, even if these are spawned by another, later male.

This is an absolute fallacy. I gained ground when we were ignorant of the true mechanism of fertilization and reproduction. Sometimes the odd claim may require further explanation only because of the male sperm can remain active for a considerable time in the genital tract of the female, and will fertilize the egg even after another mating.

Another baseless belief is that of **MATERNAL IMPRESSIONS**. The followers of this state that, for example, if your female is kept on a lean diet, her subsequent offspring will be lean, if she is kept permanently in the dark the fry will be born with impaired vision. What rubbish!

Not only is there no nervous connection between mother and fry but no connection by way of the blood. All that passes between them passes by indirect channels, dissolved or secreted through the vessel walls.

INBREEDING. To state that inbred stock degenerates on the one hand, and in another breath claim that crosses between separate strains produce strong, vigorous offspring seems a contradictory mess of facts. The curious, and at first sight, lawless statement comes from one section of Biology that in recent years has thankfully been swept clean and put in order by hard-working biologists unsatisfied with the old state of affairs.

Their findings showed that the relative merits of inbreeding and outbreeding will depend simply on the recessives which that particular strain is carrying. If these are harmful, then to inbreed with them will cause a multiplicity of faults, but outbreeding may produce good results. If they have desirable recessive, then the opposite will prove true.

PARTHENOGENESIS or Virgin Birth is now an accepted fact by forward thinking Guppy Breeders. The mass of recent evidence shows this, but this won't stop the careless fish keeper making wild claims... claims that stem usually from carelessness in his breeding tanks or lack of know-how. I can see this subject still causing a storm of argument for many years to come.

Another subject we may profitably discuss is the question of **REVERSION**. Here I would like to quote from a handbook on genetics. "It has been found that every variety that is produced artificially, if left to itself for a few generations reverts to its original type."

Occasionally, this is the case. Here though, the statement is a distortion of the truth, and I can prove it.

Reversion to type only occurs when different varieties are crossed and then left to their own devices. It never occurs in genetically pure stock.

Taking that you have learned your genetics lessons well you will realize that there is nothing very mysterious about this tendency to reversion.

The ancestral type simply turns up as one of the quite possible combination of genes which the two parents have contributed. It has little to do with evolutionary progress because the crossing of two distinct varieties is quite rare in Nature. This usually occurs when "homo sapiens" takes a hand and does it under highly artificial conditions.

To close, one question often asked me when I am lecturing on genetics, "Are the Laws of Mendelism the only laws governing inheritance?"

In the light of recent discoveries by the "Nobel" team in Great Britain, the answer to this seems to be, "not necessarily so."

Working with the Haemoglobin composition, Dr. Crick and his team have delved deep into the very heart of "what makes us tick". Their findings have enabled us to see at long last the spiral patterns of its atomic makeup. Simply, their results seem to indicate that though the whole of heredity is based on the coming together of the nuclei of the sperm and the egg. The rest of the egg protoplasm (cytoplasm) can play a part, but only further research by world biologists can say how much. Rather like being shown round a house by an Estate Agent. We examine the outside, the ground floor, but when asked to see the upstairs we are told the stairs are missing. We can see upstairs, know its there, but cannot get to it to examine it closely.

Until this evidence is forthcoming we must state that the cytoplasm having an effect is a very rare and exceptional occurrence, and in most many-cell creatures, traits are passed on by genes in the true Mendelian principles.

I have only skimmed over the fascinating subject of genetics. A subject that every guppy breeder could do well to study if it is only for the purpose of helping him to produce some "whoppers".

ATOMIC AGE GUPPIES

**Amateurs are equal to professionals when creating new varieties
luck plays a part!**

By Charles O. Masters, Wuthonburg, Ohio

Variations in guppies distinguish them one from the other in pattern, color, and size and shape of fins. Today's guppy is something hard to recognize as the one so common in aquaria twenty-five years ago. Those characteristics or modifications which are the result of mutations, to be explained later, are inherited and are of much interest to aquarists. Those characteristics caused by environmental conditions result in some variations too, but they are not inherited and are of little interest to the guppy breeder.

To elaborate about the thrill experienced by anyone discovering a new guppy variety is certainly unnecessary. Such a first gives one much pride and sure joy to successfully breed guppies and occasionally

find new mutations, one may have relatively little in the way of equipment but he should have some knowledge of genetics, much patience and a very deep interest.

New varieties of guppies can best be found in the home aquarium—look for them there. Travel to far-off places is not necessary. After some knowledge of genetics and guppy breeding is attained, it becomes possible to start "creating" new varieties. This is being done by amateurs as well as by professionals. This is true especially since luck does play an important part. In this way (i.e. appearance of new mutations) amateurs and professionals are equal.

Learn something about how guppies grow, how long they live, when they are ready to breed, and how often. Study their sexual process, which is described thoroughly in the aquarium literature. In addition, come to understand simple genetics and the general theory of evolution. Learn a little about the chemistry of life, including the effects of hormones. Basic texts on biology explain these subjects and one does not have to be college trained to master efficient, enlightened guppy breeding. Take notes and keep records, unless you do, your work may all be in vain.

Mutations, or sports, come about spontaneously so that no one can predict when they will occur. The event subsequently gives rise to a new characteristic whether it be color, shape, or size and the hereditary unit responsible is a mutant gene. The mutation of a "normal" gene must take place in either the male or female germ cells that make up a fertilized egg. The egg is then a large cell carrying this mutation. The egg cell then divides many, many times, finally forming the adult fish after growth and development. Every cell in the adult fish is a descendant of the egg cell. Genes control the developmental process and a mutant gene alters it, producing the sport or mutation such as a change in fin shape or color difference.

Not too much is presently known as to whether the change (i.e. mutation) occurs in an existing gene or as a "mistake of nature" when the gene is "copying itself" in preparation for cell division. Mutation, however, is not a slow process but takes place all at once and the "mistake" or alteration is then passed from one generation to the next because at cell division of sex cells (or any other cell division), the mutant genes like other genes, ordinarily copy themselves, passing their pattern and thus their controlling influence on development to the next generation.

To many breeders of animals, the term hybrid is commonly limited to a cross between different species but it can be used to represent a cross between races or variation of the same species so that the resulting organism will contain two different genes for the same character, whatever it might be, one coming from each parent.

Step number one to successful guppy breeding is to learn enough about their characteristics so that one can recognize new varieties when they occur. This is often possible only through familiarity with the guppy stocks in your possession. Judge what good characteristics are and be on the lookout for them. Resistance to disease and rough handling are good but they can not be seen at a glance. Keep these in mind however. It pays to study guppies in fish stores or in the homes of friends. Pay attention to both sexes and try to establish a "basic strain" by mating a female with one of her sons and thereby, through inbreeding, fixing desirable characteristics. The word, trait, in aquarium circles, is a good one to know. It is in general, equivalent to the word, character but not quite as specific. For example, one speaks of fish length which may be relatively short or long and skin color which may vary tremendously from the normal even to the point where it is a bino.

Genes are exceedingly small but they occupy a definite place on specific chromosomes (which are the inheritance controlling bodies in a cell) and control the passing on to offspring of a single trait or a combination

of traits. Each chromosome has many genes or areas controlling specific inherited characteristics of an animal or plant. By controlling the production and action of enzymes in growth, development, and maturity, genes create or tend to create the substances such as carbohydrates, proteins, and other molecules which make up cells, tissues, and organs of which the living guppy is composed. Somehow genes may be referred to as chemical groups in the chemical structure of living things but for the present the word gene is sufficient.

THE GENETICS OF THE DELTATAIL GUPPY

by Albert J. Klee, F.A.R.A.

One of the most popular tail shapes in the guppy, *Poecilia reticulata* (today is the triangle or delta type referred to from now on simply as the "deltatail"). In combination of many beautiful colors, this form has been the major reason for the current popularity of the fancy guppy. Consequently, it is of interest to explore the factors that produce such tails and their interrelationships. In this article, the following codes are used for a number of genes:

- (a) **Cc**—The **coccineus** gene. This gene is normally attached to the X-chromosome. Females with this gene have transparent tails (nonpigmented); males have only the rear-most portion of their tails transparent with the base yellowish and speckled with very fine black dots.
- (b) **Cp**—This is an **unsalted** gene. The letters standing for "caudal pigment". In the female it produces pigmented tail fins (also normal but we are concerned in this article only with the caudal fin of the guppy), resulting in grayish-to-blackish shades. In the male, it produces a tail which is colored dark blue to black. It is normally attached to the X-chromosome.
- (c) **Ch**—A recessive gene which does not manifest itself directly, but which influences other genes for tail color in the male guppy. Female guppies carrying this gene are grayish in body coloration but have non-colored tails.
- (d) **Ds**—The **doubleword** gene. This gene is attached to the Y-chromosome. It manifests itself in an elongation of the upper and lower lobes of the caudal fin of the male.

As it will shortly be demonstrated, there is **no such thing as a gene for a deltatail in the guppy**. A deltatail is produced when the male carries the gene for doubleword in combination with a number of other genes, the most important being **Cp**. To simplify things, we postulate the deltatail male guppy as consisting genetically of **XCp YDs**.

The male guppy used in the following experiments was from a Paul Mahnel strain and, under our postulate, of the genetic makeup, **XCp YDs**. The female used was of the genetic makeup **XCh XCh**. **Experiment No. 1** was to mate these two fishes. Since the **Cp** gene is displaced by **Ch** in males in this crossing, it would be expected that all males would be of the doubleword type (**XCh YDs**). **Table 1** (also see **Figure 1**) shows the results obtained. An unexpected 8.4% (3.9% of the total males and females, of the males were deltatails. It was apparent that what had happened was that the **Cp** gene of the male had

"crossed over" (see my article in the April 1964 issue of this magazine, to the Y-chromosome, forming males of the genetic makeup XCh YCp, Ds. Furthermore, the influence of Cp on the Ds gene was still effective even when on the Y-chromosome.

In order to pursue this matter of crossover further two additional experiments were made, one involving the F1 generation and another involving a backcross (see Table II). The first cross was a hybrid female (F1) of genetic makeup XCh XCo with a crossed-over male genetic makeup XCh YCp, Ds. No doubleswords were obtained, proving that the Cp gene was effective on the Y-chromosome as well as on the X-chromosome. The second was a backcross using a XCh XCh female and the crossed-over male. From this backcross, mostly doublesword males were obtained. This may be explained by the hypothesis that since the pressure is for the Cp gene to link to an X chromosome, and in the view of the fact that the female could contribute no Cp genes to prevent its migration, the Cp gene linked to the Y chromosome in the male crossed back over to the X chromosome of the females, where it "belonged".

TABLE I

Experiment No.1 XCh XCh Female vs XCo YDs male

	Females	Doublesword Males	Deltatall Males
Number	139	109	10
Percentage Observed	53.9%	42.3%	3.9%
Expected Percentage	50%	50%	0%

TABLE II

Experiment No.	Cross	Number females obtained	Number deltatalls obtained	Number doubleswords obtained
2	XCh XCo x XCh YCh, Ds	37	29	0
3	XCh XCh x XCh YCo, Ds	19	2	21

Ignoring crossover, which is relatively infrequent, the postulated model of deltatall inheritance in the guppy is shown in Figure 2. Thus, the F2 generation should be 50% females, 25% doublesword males and 25% deltatall males. Experiment No. 4 was set up to do just this (see Table III). The results were very close to expected and the actual differences from expected values were nowhere near significant (a statistical calculation of binomial confidence limits was made to determine what constituted a significant difference but these calculations are beyond the scope of this paper for those who are interested and who know something about statistics, however, the confidence level used was 99%).

TABLE III

Experiment No. 4 XCh XCo female vs XCh YDs male

	Females	Doublesword Male	Deltatall Males
Number	42	20	20
Percentage Observed	51.2%	24.4%	24.4%
Expected Percentage	50%	25%	25%
Difference	+1.2%	-0.6%	-0.6%
Significant difference	+1.7%	-1.4%	4%

TABLE IV

Experiment No. 5 XCo XCo female, vs XCo YDs male

	Females	Doublesword Males	Deltatall Males
Number	37	21	2
Percentage Observed	46.8%	26.6%	26.6%
Expected Percentage	50%	25%	25%

Because a female of genetic makeup XCo XCo was on hand, it was decided to cross it with a deltatall in order to see what effect the Co gene had on the Ds gene. One would expect that 50% of the males would be deltatall (25% of the total), and 40% would be of the XCo YDs form (see Figure 3). The results of experiment No. 5 are shown in Table IV. They do not differ significantly from that expected. One thing was of interest, however. The swords on the doublesword males were quite shortened. We must conclude therefore, that the Co gene inhibits the Ds gene. Thus, the Co gene is not only bad for color (the XCo YDs males also had yellowish tails), but bad for tail shape as well. Unfortunately it is a most universally carried by common guppies.

Also unfortunately, during these experiments the quality of the deltatalls produced, began to deteriorate in that the tails were becoming more and more uneven (as we show in all of our figures). This was due to the fact that although the Cp gene was most important in controlling the deltatall, other genes influenced also. Those were not taken into consideration. Therefore, an XCo XCo female from Experiment No. 5 (F-1) generation was backcrossed to the original male P or parent generation to produce an F-2 deltatall male (the shortened doubleswords were discarded). Then, an F-1 female of genetic makeup XCh XCo from Experiment No.1 was selected. Crossing the F-2 male with the F-1 female mentioned produced the usual 25% deltatall males and 25% doublesword males (actual percentages were 23.4 and 25.0% respectively but the deltatalls were now quite good. The inbreeding was evidently retarded those genes other than Cp that are essential for producing quality deltatalls.

In conclusion, we may make the following statements:

1. There is no gene for deltatall in the guppy. Rather it is caused by a combination of doublesword gene (Ds) and a number of other genes, notably Cp.
2. The coeruleus gene is bad from both a color standpoint, and from the standpoint that it suppresses the doublesword gene.
3. Crossover of the Cp gene from the X chromosome to the Y chromosome takes place infrequently resulting in a small number of deltatalls, where none are expected. Most likely, this was one of the major factors in the original introduction of the deltatall.
4. Only in the infrequent case of a male crossover, may one ignore the female in the production and maintenance of deltatalls. At all other times, the female carries the all important gene, Cp, which is the major influence other than Ds which is carried by the male only in producing deltatalls.
5. Although the Cp gene is most important in influencing deltatall strains, such strains will deteriorate unless some inbreeding is practiced. This preserves other Ds influencing genes in the strain.

References: Dzwilo, M. "Genetische Untersuchungen an domestizierten Stammen Lebnestheula" Mit Hamb. Zool. Mus. Inst. Bd. 143-186, 1949 and Klee, Albert J. "Genetics of the Guppy" Aquarium Magazine, Vol.33, No.4, pgs 26-31, April 1964.

NON SEX-LINKED FACTORS IN THE BODY COLORATION OF THE GUPPY

by Albert J. Klee, F.A.A.

The skin of an ordinary guppy contains a number of different pigment cells, foremost among these in both sexes being melanophores (i.e. black pigment carriers) and xanthophores (i.e., yellow pigment carriers). For the breeding of specialized strains of guppies, it is desirable to learn something about the genetic characteristics of these pigment cells and the "how" and "why" that provides a better understanding of guppy inheritance in general. We will be concerned only with non sex-linked heredity pertaining to body color (thus we exclude "black" which is sex-linked).

There are a number of descriptive terms used by aquarists with regard to guppies among them being "gold", "blond", "cream", and "albino". Basically these terms are not directly linked to the number and form of melanin-containing pigment cells (melanophores). The scales of an ordinary guppy contain what are known as "dendritic" melanophores. These are branching, tree-like structures. The body of the guppy contains melanophores also, but these are shaped far differently. Two kinds can be observed, viz., "corolla" melanophores, so named because of their flower-like structure, and "punctate" melanophores, named for their dot-like appearance. The former are large, the latter very much smaller.

Gold, blond and cream guppies do not differ much in the nature of their dendritic melanophores except that these melanophores are somewhat larger in gold guppies.

The fundamental difference between a "wild" type guppy and a gold guppy is that in the latter the number of melanophores near the surface of the skin is reduced approximately by one-half (with an attendant enlargement to some extent). There is some evidence also that leads us to believe that the gold guppy has a greater number of xanthophores than does the wild type. However, xanthophores are hard to count so that the quantitative data upon which this surmise is based is in some doubt. There is a gene for gold and it is autosomal (i.e., it is not on a sex chromosome). Furthermore, it is recessive to gray (the wild or ordinary color). We speak of alternate phases of a gene as "alleles." Thus, if gray is allelic to gold and vice versa, what we mean is that there is a gene called "gold" and it exists in two phases, one, a dominant phase reflected by the fact that then the guppy is colored gray, and the other, a recessive phase reflected by the fact that then the guppy is gold-colored. Since the gold gene is autosomal, both males and females may carry it. The gold gene follows the very simple Mendelian laws that we have mentioned in the past, i.e., if we cross a pure gold strain with a pure gray strain, the offspring would all appear gray. Then, if we interbred the F₁ generation, the F₂ generation would be gray to gold in the ratio 3:1. This is illustrated by the device of the square shown in Table 1 (g - recessive gold phase, G - dominant gray phase).

The gene for blond is very similar in that it is recessive to gray and is also carried on an autosome. Furthermore, it is carried on a different autosome than that of the gold guppy. The fundamental difference between gray and blond guppies is not in the number of melanophores but in their form. The body melanophores of both gray and gold guppies are corolla type while those of the blond guppy are punctate. Thus, the gold gene is a melanic suppressor while the blond gene is one which basically alters the form of the body melanophores. Blond, therefore, is not allelic to gold.

Since the genes for gold and blond are carried on different autosomes, both may occur simultaneously, if this occurs, then we obtain a cream guppy. Not only do cream guppies have a reduced number of melanophores, but the body melanophores are of the punctate type. Thus, there is no such thing as a gene for cream, it is the result of the simultaneous occurrence of gold and blond. Cream guppies are very nonviable,

the combination of gold and blond genes proving lethal to some degree. Blond and cream guppies are very similar in outward appearance, the former being more yellowish in general, however.

Another gene that suppresses melanin (and not only in the chromatophores but elsewhere as well) in the guppy is the gene for albino. Like blond and gold, this is recessive to gray and is carried on an autosome. Also, it is carried on an autosome different from that of either blond or gold. Consequently a guppy may carry genes for all three, viz. gold, blond and albino. Albino is a highly lethal gene (regardless of statements I have seen recently in the aquarium literature). Among other things the effect of the albino gene is to eliminate dendritic corolla and punctate melanophores from the guppy. Consequently, although it has no genetic linkage with blond or gold, i.e. it is not allelic to them, it "overrides" both of these genes in effect, except that the gold gene may provide a greater number of xanthophores than an albino guppy might ordinarily have.

TABLE I
hybrid male (g)

hybrid female (G)		G	g
		GG (gray)	Gg (gray)
hybrid female (G)	g	Gg (gray)	gg (gold)

TABLE II
hybrid gold male (appears gray), GgAa

hybrid albino female (appears gray) (GgAa)		G		g	
		A	a	A	a
G	A	GGAA gray	GGAa gray	GgAA gray	GgAa gray
	a	GGAa gray	GGaa albino	GgaA gray	Gga a albino
g	A	GgAA gray	GgAa gray	ggAA gold	ggAa gold
	a	GgAa gray	Gga a albino	ggaA gold	gga a gold-albino

Double genetic systems are very interesting. Suppose one mated a hybrid gold guppy as shown in table II (g - recessive gold phase, A - dominant gray phase). The following offspring would appear albino: Ggaa, GGaa, Gga a, the following would appear golden: ggAA, ggAa and ggAa. This leaves gga a and gga a others, resulting in the familiar 9:3:3:1 ratio for simple Mendelian double systems. Actually, the gga a would also appear albino since the gene for gold could not express itself except for an increased number of xanthophores. Very few, if any, would survive because of its inherent non-viability. To a lesser extent, this holds true for the other albino offspring also.

The gene for blue is likewise carried on a separate autosome but is not allelic to gray but rather to genes for yellow and red. We are talking now about the general blue body coloration, and not isolated areas of brilliant blue in various forms. The blue gene is a suppressor of yellow pigments (red also, but these are generally carried on sex chromosomes and are outside the scope of this article). Thus, gray guppies appear blue and blond guppies appear white if the gene for blue is present.

Suppose for example, that we cross a blond guppy with a blue guppy. The F-1 generation would then all appear gray. If we inbreed this F-1 generation, the F-2 generation would appear gray-to-blue to blond to white in the ratio 9:3:3:1, in accordance with simple Mendelian laws of a double system (see Table III—recessive blue phase, R—dominant gray phase, b—recessive blond phase and B—dominant gray phase).

We may therefore summarize what we have learned as follows:

1. Ordinarily, both sexes of the guppy carry melanophores and xanthophores.
2. The Common guppy has body melanophores of the corolla type.
3. The gene for gold is a recessive allele to gray, carried on an autosome. It manifests itself by an approximate 50% reduction in body (corolla, melanophores).
4. The gene for blond is a recessive allele to gray, carried on an autosome. It manifests itself by a transformation of body melanophores from the corolla type to the punctate type.
5. There is no gene for cream; rather, it is the simultaneous occurrence of genes for gold and blond. The conclusion is somewhat lethal.
6. The gene for albino is a recessive allele to gray, carried on an autosome. It manifests itself by a complete suppression of melanophores (both skin and scales). It is decidedly lethal.
7. The gene for blue is a recessive allele to genes for yellow and red, carried on an autosome. It manifests itself by suppressing yellow and red pigments.

TABLE III
hybrid blond male (appears gray), BbRr

		B		b	
		R	r	R	r
hybrid blue female appears (gray) BbRr	B	R	BBRR gray	BBRr gray	BbRR
		r	BBBrr gray	BBrrr blue	BbBrr gray
	b	R	BbRR gray	BbRr gray	bbRR blond
		r	BbBrr gray	Bbrrr blue	bbBrr blond

A LITTLE BIT ABOUT A BIG SUBJECT

by Joe Sten,uk

GENETICS

Johann Gregor Mendel lived from 1822 to 1889. He was an Austrian Monk and botanist and is recognized as the founder of the science of Genetics. To begin with, let us state the 3 principles of heredity better known as Mendel's laws.

1. THE LAW OF INDEPENDENT CHARACTER UNITS states that characteristics such as color, size, etc. are inherited separately as units.

2. THE LAW OF DOMINANCE states that in every individual there is a pair of determining factors for each unit character. One from each parent. If these characters are different, one character (the dominant) appears in the offspring, the other being recessive remains latent. The recessive character can only appear when the dominant character is absent, hence in all crossbred generations, unit characters are shown in various combinations, each appearing in a definite proportion of the total number of offspring.

3. THE LAW OF SEGREGATION states that body cells and primordial germ cells contain pairs of such unit characters and when gametes are produced, each gamete receives only one member of each such pair.

Let's dwell on **rule # 2** for a moment. The definite proportion Mendel states of 25% - 50% - 25% - 00% of the offspring. Suppose we breed an albino fish (we will call A) to a gray which we will call G. Now let's go a step farther and breed an AG to an AG. We obtain 3 gray to 1 albino, 1 GG - 2 AG - 1 AA.

If only we understood this law completely, what beautiful guppies all of us could have, we could purchase a Best of the Show winner and in the third generation reproduce him perfectly. I am sure we all have tried something like this sometime or other and were disappointed in the results the majority of the time. Many books on Genetics mention a fallacy, that the average layman is guilty of in respect to Mendel's Laws. This is called "Oversimplification of Mendel's Laws of Inheritance". We are wrong to believe one gene determines one potential. Geneticists are now aware that many, or perhaps all, genes and their spacing on the chromosomes may determine potential. A guppy has twenty-three pairs of chromosomes. Each chromosome has many genes, the possible combinations and possible spacing could reach an amount that would stagger the imagination.

There is another error we could be guilty of in breeding guppies. This is to believe that a certain gene is dominant, and always held sway. It is now recognized that dominance is relative rather than absolute. One example is brown eyes in man are dominant over blue, but blue eyes in man are dominant over red or pink eyes (albinism). Another example is in livestock. The white-faced Hereford with its white face and red body is wholly dominant over whatever its recessive genes contain. Yet when we cross a red shorthorn to a white, we get a man, a combination of red and white. How about the beautiful multi-colored guppies we all have seen. I wonder which color is dominant. It would appear that the geneticists who maintain dominance is relative rather than absolute are correct. In the reproduction process there are certain chromosomes, called **Reduction Division Chromosomes**. A cell containing two chromosomes divides, and two new cells were formed, each cell received half. This is called a gamete. When a gamete from a male is united with a gamete from the female a zygote is formed (fertilized egg). The zygote contains a full complement of chromosomes, one-half from the male and one-half from the female gamete.

An organism with one trait (Aa) could produce two different gametes, A or a. An organism with one y two traits could produce 4 different gametes. An organism with 3 traits can produce 8 different gametes, four traits — 16, five traits — 32, six traits — 64 and so on up the scale. Thus an organism with only ten traits can produce over 1000 different gametes, and twenty traits well over a million different gametes. Just think, guppies have 23 pairs of chromosomes, hundreds of different traits. This can make the genetic variation possibilities practically boundless. (Preprinted from Spritely Subjects — March, 1967 issue)

BREEDING THE GUPPY

by Bill Thompson

In all fishdom there is nothing quite like the guppy. This tiny creature is bred and developed by both the rank amateur and by the advanced hobbyist. These two classes breed them with different objectives, of course, but it is still the same tiny fish of many surprises.

Guppies do not require a lot of space, but bear in mind that all fish are happier when they have plenty of room. For this reason we recommend that they be kept in a ten gallon or larger aquarium. The water in this aquarium should be slightly alkaline. Old water is desirable but not essential.

You will find that the guppy reacts very readily to temperature changes. Any sudden rise or fall will weaken the fish and may induce disease. The larger tank will nearly eliminate this possibility. Of course, optimum temperature for the guppy is described as one between 70 and 78 degrees F.

The guppy is also easily suited to foods. Any prepared variety will do, although it is best not to stick to those containing a high percentage of animal meal. Shredded shrimp heads the list of prepared foods. Other suitable foods are finely chopped beef, lobster, clam or salmon or of course the live foods, worms and daphnia.

Probably the questions asked by most beginners deal with the absence of color in the female while the male is so colorful, or how many young the females may have at one time, and how are the young born?

In answer to the first, although the female bears little or no color herself, she is equally important with the male in determining the coloration of the male offspring. Like birds and mammals, this lack of bright colors is probably protective, since tests have proven that coloration identical to that of the male fish is latent in the female, and only an injection of male hormone is needed to bring out these colors.

The number of young offspring born by any one female varies with the age, size, and condition of the female. Average broods may run between ten and fifty.

Young guppies are not born in the same sense that mamma young are born. While in both cases the eggs are fertilized and developed within the female, the similarity ends here. The female mamma nurtures the developing embryo as it grows, and the offspring is much larger by comparison. The eggs within the female guppy, however, receive no nourishment from the female. The embryo simply develops within her until the yolk sac is absorbed. Then the fry are born.

It is interesting to note that the viviparous fishes, those which bear young in the manner described above, bear relatively few large and well developed young as opposed to the thousands in many cases spawned by the egglayers. Here surely is protective environment at work.

Good guppies do not just happen. They are the product of months, even years, of extensive research and development. No person who is not prepared to be patient, painstaking in his methods and ready for disappointment should endeavor to one breed guppies or any other fish for this matter.

One local guppy fancier has explained the following method to the writer. At the outset to fix his strain, he takes the best male from the first batch of fry F-1 and breeds him back to his original female. He then takes the best six females from the same hatch and breeds them back to the original male. The resultant spawning will be the second generation of the young G-1 (not F-2). Once again the best male of the brood is bred back to the original female P-1 x G-1 — G-2. This operation is repeated once again to produce the next generation P-1 x G-2 — G-3.

This whole procedure serves one purpose: to fix the strain and is called inbreeding, as is close breeding between father and daughter or mother and son. This inbreeding is the best means of developing and establishing a strain. But this advantage is not gained without risk, the risk of greatly weakening the strain. By selecting vigorous offspring this may be partially offset.

Having established his strain, this breeder then proceeds to one breed his fish in a way that emulates the basic principles laid down by Gregor Mendel, one hundred years ago. All guppy breeders, whether they are conscious of it or not, utilize these laws of nature that Mendel discovered so long ago.

Since all guppy breeders use Mendel's Law, then it will help all concerned to know the rudimentary principles of heredity.

All living things exhibit influence of two major sets of characteristics. One of these is **environment** and the other is innate **biological make up**. Environment exerts its influence from outside and consequently has no place in this discussion. However, biological influences exert their control from within and are primarily transmitted from generation to generation by hereditary factors called genes. This is done in all living things and results in the appearance of specific traits in an individual fish.

Mendel laid down three basic laws. These are defined as follows:

- 1. The Law of Dominance:** When two pure bred fish with contrasting characters are crossed, all the offspring of this mating will show only one of these two characters. The character that appears in the first generation is called dominant and the other character which is invisible, is termed recessive.
- 2. The Law of Unit Character:** The various characters or traits that appear in an organism are transmitted to the offspring as distinct, individual traits without being changed or lost in any way.
- 3. The Law of Segregation:** The hidden, recessive character in a hybrid organism may be segregated in a later generation. When two hybrids are mated, the resulting offspring comprise from any one character **pure dominant 25%; hybrid offspring 50%; and pure recessive 25%**. This is frequently called the 1:2:1 ratio. Successive generations of hybrids yield the same ratio.

We will deal first with the **Law of Dominance**. Suppose a veiled male guppy is crossed with a common female guppy. All the offspring from this union will exhibit the characteristics of the common guppy. However, when two of the offspring are mated, the fry from this mating will obey the Law of segregation.

Since each of the original parent contribute one gene each to the cells of the offspring, the cross of CC (common female) x vv (veiled male) — Cv (common F-1)

F-2 Cc x Cc — 1 CC 2 Cc 1 vv

At this point we return to a discussion of the technique of breeding used by the local breeder mentioned previously. Since this breeder could not safely assume that his initial parents were true breeding

types he found it necessary to breed to the third generation of fry to establish and fix his strain. Continuing our discussion from the veil tailed male developed as shown on previous page is simply to do what the local breeder did. By selecting the true veil tailed male and a veil tailed gene carrying female from this generation and mating the two to continuous line breeding, we have insurance that all offspring will be veil tailed. However, there is one stumbling block. A veil tailed female cannot be discerned from other females. Hence, it is necessary to isolate each female from this spawning and cross with a veil male. The fry from this spawning must also be isolated so that the breeder may ascertain from the fry which female was the true veil tailed. Once this is established we have a true breeding fixed strain of veil tailed guppies. A testcross of $VV \times CV = 50\%$ veils, $VV \times CC = 0$ veils. Best of luck with yours.

Reprinted from Guppy News Dec. 1963

GUPPY POINTS TO PONDER

by Arthur Lietz

One of our Bay Area aquarists had a disconcerting experience a few months ago. He imported some albino Guppies from New York and crossed them with his own line of albinos in the hope that his outcross would increase the vigor of his fish. All the babies were silver. Not one albino in the lot!

Naturally he was unhappy over this but as it happened there is a perfectly good explanation. It has to do with the mechanisms by which a fish inherits its body characteristics from the parents. Every living thing is a complex chemical factory, with each of many hundreds of chemical processes going on at the same time, some in sequence with each other, some in balance with each other. Often the failure of just one of these processes will cause death!

A Guppy has to inherit, from its parents the exact recipe for carrying out each process. These recipes are vitally necessary to the offspring's survival. In these circumstances, the prudent thing is to have two copies of each recipe and this is just what happens. The guppy inherits one gene from its mother and one gene from its father. The genes from each parent are bound together for greater protection against loss. Guppies inherit 23 chromosomes from each parent or 46 chromosomes in all.

Now the production of dark skin pigment, called "melanin" from its raw material, called "dopa" involves 6 different chemical steps. Dopa is necessary for higher animal life, but so far as I am aware, the six substances produced in these six chemical stages in the production of melanin from dopa include "Process K" and "Process S" (just to call them something without tying ourselves down as to which steps they are).

A Guppy which has all its genes with the exception of one gene of process "K" will go right ahead and make melanin. Process "K" will operate at half efficiency because one of the two genes are missing but this will just make the Guppy a little paler, not enough to notice. But a Guppy which did not get any gene of process "K" from either parent will be completely unable to make melanin. It will have no dark pigment in its skin or in its eyes and will be an albino. The same goes for process "S". A guppy which is missing both its genes of the process will also be an albino.

Supposing, however, that someone comes along and crosses these two albino Guppies with each other. The one without process "K" will give all its babies one gene "S". The one without prod "S" will give all its babies one gene of process "K". Therefore every baby will have one copy of process "K" and "S". Both process "K" and "S" will be working at half efficiency, for an overall efficiency of about a quarter. The fish will definitely be paler than ordinary guppies but they still would not be albino. Thus, my friend's silver guppies.

If he had gone on, however and crossed his silver guppies with their brothers and sisters (assuming gene K and S are bound into different chromosomes, 3/16 of their offspring would be missing both genes of process "K" and be albinos, 3/16 would be missing both genes of process "S" and be albinos; and 1/6 would be missing both copies of process "T" and both genes of process "S", and be super-albinos. The super-albinos, probably would not look any different from the regular albinos, unless they were paler, but they would be there and could be found by a series of test cross with the pure grandparent stocks.

(Reprinted from the Anchor Dec. 1967)

SO YOU WANT TO RAISE GOOD GUPPIES

by Henry Kaufman

About three years ago, a radically differently colored guppy from what we had become accustomed to seeing suddenly appeared on the American market. At first it was called the German three-quarter black or German half-black. Today we refer to these guppies as the three-quarter and half-blacks. The difference being that in the three-quarter black the male's body is three-fourths black and the dorsal and caudal fins are a bright red, and the half-black is half or less black but it still has the bright red coloration in the dorsal and caudal fins. The females of the three-quarter blacks have a solid black covering three-fourths of the body. Most of them have solid black dorsal and caudal fins, but in some of the poorer specimens, the dorsal and caudal are a deep grey with some black spots. The female half-blacks have half-black bodies with grey tail and dorsal in the better specimens. The others have a deeper grey cast than what we see in our regular guppies, covering the entire body, and have dark edging on both the dorsal and caudal fins. In some cases they also carry black spots on both fins.

These fish with their dark black bodies and bright red fins were eye-catching and were eagerly sought after. I must admit that as soon as I saw them, I was eager to acquire some stock. I first came across them when visiting a well-known hatchery in Florida. Although the owner had quite a number on hand, he was unwilling to part with any. He eventually agreed to let me have two males but no females, and since the males he offered were far from the best on display, I did not accept the offer. I next ran across them while judging a show in Cleveland, but the breeder said that those on exhibition were his only good specimens and he was unwilling to part with any. He claimed that his stock was not breeding true. During the next few months, I ran across over a dozen breeders who had the strain, but their stock was of such poor quality compared to what I had previously seen that I did not think it was worth the effort to try to improve them. Shortly afterward, while attending a show in California, I was fortunate to see a breeder who had some fairly good specimens and since he was just as eager to acquire some of the fish I had on exhibit, we traded stocks.

I hurried home with my newly acquired three males and six gravid females and within a few weeks I had several hundred young fry. Unfortunately, as is the case in many new acquisitions, only about one-tenth of the young were of the same pattern as the parents. The balance consisted of at least a dozen different kinds ranging from swordtails, plain reds, blues, and gold guppies, and practically all of them could be classified as culls or mixed breeds. I was able to get about five hundred young from four successive breedings but these too turned out to be the same as the first batch. Out of about seven hundred that I was able to raise from the parents, only about fifty resembled the originals. Of these fifty, thirty were poorer specimens than the parents, ten were equal to the parents, and ten were just a wee bit larger in body and finnage. The ten that were equal and the ten that were superior were placed together at the age of four months and within a short time I had several hundred more fry. Being very careful to separate the males

from the females when they were less than two weeks old. I eventually raised over seven hundred babies from this lot. There was considerable improvement in the number breeding true since nearly half were kin far to the parents. From this lot I was able to pick several dozen for my next round. At this point, I was not determined to come up with large fish of this strain, and I now set up five different breeding tanks of the best specimens of the lot. Being careful to keep the fry of each different tank separate, I was finally able to raise several thousand fish with the same color pattern as the original parents. At this point, I sat down to evaluate the whole program to see what I had accomplished.

The strain was now breeding fairly true since nearly seventy percent were like the parents. However, there were several results which I could not accept. The males of these three-quarter blacks, even with prime living conditions such as the best of foods and more care than I was giving the rest of my fish, were not satisfactory. They retained the same black body, the dorsal and caudal fins were just as bright red as ever, but the body had not increased in size to any appreciable degree. The same was true of the dorsal and caudal fins. Upon close examination of both my fish and the same strain that over a dozen other breeders were raising, I came to the conclusion that the body of this type fish seemed to have that emaciated look that made me believe in spite of the high protein diet I supplied that this strain could not carry a large tail, even if it grew one. The tails of a lot of male specimens eventually grew at least as high as one-half inch and a few even acquired tails three-quarters of an inch high. At the same time, the males remained perfectly straight until they reached the one-half inch size but from here on over 75% acquired ragged edges and started splitting. Most of them soon wound up with what you might call shredded instead of split tails. You had to raise a thousand fish to get a half dozen which were of show quality. This same result showed up with every one of the breeders I knew of who were raising this type of fish. To me this result was a waste of time and effort which could be used in producing other good fish. If after raising several thousand fish of any strain, you come up with a true color pattern but no marked improvement in body size and finnage, you can safely assume that there will likely never be too much more advancement. Any potential good strain should have at least five to ten percent of the young fish turn out to be better specimens than their parents. This condition should prevail for as long as you have the strain. When it ceases to exist, your strain has reached its maximum potential for size. In the case of my regular multi-blue and green strains, this condition still exists after 15 years and every new generation shows more and more fish which are better specimens than their parents.

However, I did notice one good result in the three-quarter black fish I had raised. The females I now had were at least half again as big as the original ones. Many were double the size and a few dozen were nearly as large as my jumbo blue and green females. Most of these jumbo females still retained the solid black dorsal and black caudal fins as well as the three-fourths black body.

With my evaluation of this fish in mind, I now decided to attack the problem of getting larger three-quarter blacks with a new crossing. Just to prove to my self, however, that I had not given up too early on the original fish, I kept six trios of my best specimens. After three more generations, taking care to select the best of each one, I can still report the same results. The strain now breeds more true.

I then crossed my blues with this black strain and obtained F-1 fry that had a much deeper greyish appearance and carried a few black spots in the caudal as well as dark edgings in both the dorsal and caudal. One third were half black females with a deep grey in the caudal fins. The other third were three-quarter black females. Half of these had deep grey dorsal and caudal fins and the rest had jet black dorsal and caudal fins. Some of both kinds also showed distinct green spots and edging in both fins. I might also add that under a side light at this age both the males and females all showed green in the head and gill section which later developed into a beautiful shade of green.

In the multi-blue cross, we ran across a different group of colors in the males. There were the usual blue type males with a deeper blue color and black patches in the body and fins. There were quite a few veil-tails that had three-quarter black bodies with black dorsal and caudal fins. There were about ten percent that looked like the original three-quarter black with red dorsal and caudal. These had much larger sized bodies than any of the original strain. The rest were all three-quarter black bodies with variegated red, pink, and blue dorsal and caudal fins. The red spots covered the entire caudal fin and were very predominant. Here too it was very apparent that all of the males had acquired some body size from the male parent since they were as large as the original variety when only three months old. The females of this group were just about the same as the females of the green cross. One third were dark grey, one third half black with deep grey in both fins and the rest three-quarter black with the majority having black dorsal and caudal fins. However, no spots or edging color appeared in any of the females as we had in the green cross.

All of the fish of both crosses were allowed to grow until they were five months old at this time, owing to the crowded condition of my hatchery and also to the fact that I had some new and different colored guppies of very good size and finnage, I now had to make a choice of new breeding stock for the next round and get rid of the rest.

I now decided to eliminate all the fish with the exception of three kinds. The three-quarter blacks with green dorsal and caudal, the three-quarter blacks with variegated red and blue fins, and the three-quarter black with black dorsal and caudal. Right now, some of you will wonder why I have not originally started out to improve the three-quarter black with red tail and dorsal, and since I admit having acquired a number of better specimens from the cross than my original stock, I was now dropping this variety. The reason is very simple. First of all I can only carry a limited number of different fish and a limited number of experiments, and since all the three varieties retained were larger body size and showed more promise, I decided to concentrate on these. Another factor which determined my decision was the fact that in practically every strain of fish I had ever seen, the variegated colors are always the ones with the largest body size and finnage size. The solid color strains do not grow as large in comparison. I firmly believe that if you strive for a solid-color fish, you will always have to sacrifice potential size in body and fins. Since body size is also the determining factor in the saleability of a fish, I also considered this factor in determining my decision.

Accordingly I now set up two tanks each of the green cross and red variegated cross with ten males and twenty females in each. Because I did not have enough good specimens of the three-quarter black variety, I set up one breeding tank of this variety. At this point, because I was still retaining a few trios of the best of my three-quarter blacks with red tail and dorsal from the blue cross and since I had also retained the best of my original stock, I felt that at any future time I could resume these experiments.

Needless to say I again selected the best available specimens of each variety. As a point of interest, I might state that all fish selected were at least double or more in body size than any of the original three-quarter black with red fish that I started with. At this height, at five months, of more than one-half inch but not quite three-quarters of an inch.

I now awaited the results of the second round, and here again I was more than pleased. In the green cross, the solid green males are down to ten percent. The rest are all three-quarter blacks with variegated green dorsal and caudal fins. There are still about two percent swordtails in the group. Body size, at a comparative age is at least as large or possibly a little bit larger and about 20% of the males show better body size than the breeders. These look as though they will grow bodies as large as my blue or green varieties. The same holds true for the females. One fourth are the kind with deep grey body and spots in both fins and the rest are all three-quarter blacks. Half of these have light black tails and half have deep jet black tails.

In the red variegated cross, while the improvement is noticeably marked in the females, the males do not show quite as great a change. Most all of the males show a body at least a wee bit larger and ten to fifteen percent show even larger size than their parents but the advance is not as spectacular as in the green cross. However, I am positive that with the fairly large numbers that do show larger bodies, I will soon be able to show fish of this kind with three-fourths to an inch high tail. It is simply a matter of time and a few more selective generations.

In the white three-quarter black body and fins, the young are mixed. About half are solid black and half have variegated colors with considerable black. Body size is about the same as the parents with only a few showing the possibility that they will grow tails of more than a light over one-half inch. I am still however, going to continue this line for a few more generations.

Of greatest interest in the whole experiment is that in one of the green three-quarter tanks, after raising about 150 males in a 50 gallon aquarium, I find one very outstanding male. These are, at four months of age, double and triple the size of even any jumbo fish I have ever raised or seen elsewhere. Once in a while, at some of the shows, you see a large sized male which, although he has a gonopodium and large tail, has a body which is very similar to a female's in size and has less coloring than the regular males carry. These are commonly referred to as mules. Mine are not this type. The ones I have are exactly like the regular males in all appearances, except that they are extremely large. At present, I have five of these males. I have set up one ten-gallon aquarium with two of the males and eight females and one 20 gallon aquarium with the same number of fish. The females selected were the largest and blackest ones from the same hatch that the males came from. One male at present is still with his smaller brothers and I will keep him so for a while longer. At the time of this writing, five of the females in the ten-gallon tank are gravid but only one in the 20 gallon tank is. I will probably switch these to a ten-gallon tank, where it will be easier for the male to catch these very active females. Just as soon as I get young of suitable size, I will report further on this fish. It is just possible that I may be achieving a breakthrough in guppy size. In the meantime, anyone who cares to, is free to make an appointment and come to see these and other fish. Unlike many breeders who tell me about what they have but do not invite you to see them, I am proud of my specimens and will be delighted to show them off.

- reprint from THE AQUARIUM, May 1966

NEW STUDIES ON DOMINANT AND RECESSIVE GENES

reported by Astrid Young

In the June 1982 the Austrian Guppy Association organized the International Guppy Breeder Meeting in the Lower Austria in Lower Austria. The theme of this workshop was "Guppy - body size and coloring". We also wanted to acquire new connections of dominant and recessive genes of guppies. The start of the recessive color "Silver" was commented on by an article written by Hans Luckmann, author of the book "guppies" published by Kosmos Vivarium, Germany in 1978. Luckmann is a member of DGR e.V. Germany. He explained his latest findings on Silver as follows:

We expect every guppy breeder to know the single recessive colors. From crossing the single recessive color Blond and Gold the double recessive color Cream develops. From crossing the single recessive colors Blue and Blond develops the double recessive color White, which was described by Dr. Wille for the first time.

A new attempt of crossing was practiced by Hans Luckmann and other DGR breeders with Blue and Gold. The F1 was undivided Grey. In the F2 the real number of the guppy fry was very near the theoretical number: about 57% Grey, 18.4% Blue, 17.2% Gold and 6.9% a new basic color. The theoretical relation of 9:3:3:1 should be as follows: 56.25% 18.75% 18.75% 6.25%. It was established that from the 4 basic colors which appeared in F2 the guppies with basic color Blue were very weak, they were even weaker than guppies with the new double recessive basic color. The strongest fish were the grey ones, nearly as strong were the golden guppies.

At the fertility the succession was changed, Grey propagated best with one another. Gold with Gold produced only few descendents. On crossing recessive guppies with grey partners the crossing Grey with this new basic color brought the best results followed by crossing Grey with Gold. The new basic color is similar to the basic color white. But the fish have such body scale edged in black, thus the guppies have a darker appearance. This basic color emerges not so clearly as Blond, Albino or White, for example. It looks like tarnished silver on photos or at certain incidences of light. For this reason, Hans Luckmann decided to name this double recessive color "Silver". Silver was integrated into the IHS rules in 1981 as a sign of progress of guppy hybridizing. But, the breakthrough on this basic color at shows must be left for the future.

THE GENETICS AND BREEDING OF GUPPIES

By Albert J. Klier

It is surprising that the genetics of the guppy are quite different from those of other aquarium fishes. Primarily, the guppy is unique in the degree of the frequency of sex-linked and sex-influenced genes associated with its genetic history and in view of the vast amount of interest nowadays in breeding fancy guppies, it is of interest to review the genetic mechanisms that may be encountered in such programs. It is also apparent that few guppy breeders fully understand these mechanisms or appreciate how they may be applied to their final objectives. Since such objectives are set on a personal basis, this article will summarize in the shortest space possible, the mechanisms only, leaving the reader to tailor his breeding programs in the light of these mechanisms as they may be applicable. As for the reader, it should be emphasized once again that the hobby can advance only if proper records are kept, for it is a hard fact that the results of selective breeding are of value to other aquarists only when sufficient documentation is available to permit independent duplication of individual successes.

SIMPLE MENDELIAN INHERITANCE is, in its turn, a reflection of simple probability laws. By such inheritance we mean that the parent transmits to the offspring a random one of its two genes. This is nicely demonstrated by a consideration of a recessive mutant trait of the guppy known as golden. Such a condition is one in which there is approximately a 50% reduction of the melanophores characteristic of wild populations. In short, this loss of black pigment cells makes visible the underlying yellow pigment cells (xanthophores) present in the skin of all guppies, resulting in the production of a distinctively bronze general body coloration with conspicuous black reticulation (further reduction of black pigment results in blond and cream guppies, characterized by a light, unmarked yellow-silver to yellow coloration. These also are recessive to the natural wild or gray state). According to the Mendelian theory, the expected 3:1 ratio wild to golden is observed in the F2 generation. Golden, blond and cream are what are called

autosomal y-linked traits. An autosome is any chromosome other than a sex chromosome. Therefore inheritance of these factors is not linked to sex and the mutations affect the body color of both sexes equally.

SEMILETHAL GENES If we now consider a seemingly a most identical case, however, the results are quite different. Suppose we mate an albino guppy with a wild one. Albinism in the guppy is like golden, a recessive mutant trait. Surely the F₂ results must be identical, i.e. a 3:1, wild to a bino ratio? We find, however, a 53:1, wild to albino ratio! The explanation is simple. Albinism is a semilethal mutation that has associated with it, a high mortality of the fry prior to birth. Actually, golden is also a semilethal gene and the actual F₂ ratio is much greater than the 3:1 given in the previous section.

SEX-LIMITED INHERITANCE: Another interesting type of inheritance in the guppy is the simple Mendelian sex-linked type. The pattern of 2 to 5 bars on the rear portion of the body of males is known as the zebrianus (Ze) pattern. This pattern (a dominant one, carried on an autosome) is only visible on males although females may carry the gene for it, therefore, only males show the pattern although both sexes may be zebrianus carriers. Now let us attempt a "back cross", i.e., we mate a P-1 non-zebrinus male with an F-1 zebrianus carrier female — 50% Ze carriers and non carriers. Thus, the zebrianus pattern may seem to appear from out of nowhere because of this sex-limited inheritance and does not show in the female phenotype.

SEX-LINKED INHERITANCE: We arrive now at a consideration of sex chromosomes in the guppy. In mammals, the female is homogametic XX and the male, heterogametic XY. In birds it is the other way around! Both systems are represented in fishes, but sex determination in the guppy appears to be of the XX female, XY male type.

It has long been known that a dominant color trait in guppies, a black spot in the dorsal fin plus a red body spot (known as maculatus) is inherited only from father to son. As it turns out, the maculatus gene is ordinarily carried only on the Y chromosome and thus we have sex-linked inheritance. The mechanism is, Mu, in all males and colorless in all females. Therefore, such a gene, if present can never be hidden as in the case of merely sex-limited genes.

CRISS-CROSS INHERITANCE occurs when a gene is transmitted from a father exclusively to his daughters or from a mother to her sons. However, in the guppy, crisscross inheritance may appear to be nonexistent because females are not capable of expressing the color or pattern characteristic of its genetic makeup. In the lutinus (Lu) form (a yellow form... note that scientists have given names to a number of color and pattern forms among which are armatus, pauper and coccineus-vitelinus, but there are many others) of the guppy the father transmits this gene only to his daughters (and the mother, only to her sons) and thus represents true crisscross inheritance. Such daughters do not show the lutinus pattern, however, unless they are masculinized by hormones. The use of methyl testosterone, a standard technique among fancy guppy breeders, brings out the color in lutinus females.

CROSSOVER: Crossing over of the sex chromosomes has been observed in the guppy. For example, although the maculatus gene is ordinarily linked only to the Y chromosome, it may on rare occasion, cross over to the X chromosome (actually, only a portion of the maculatus pattern is subject to crossover, that part involving the dorsal pigmentation only and not the red body spot). Again, because this is sex-limited, the pattern will not be evident in such females unless they are masculinized.

ALLELISM: An allele represents one of several alternate phases of a gene. Furthermore, instead of one gene having just two phases, one dominant and one recessive, the gene may have two or more expressions in its dominant phase. There is some evidence that patterns such as maculatus, pauper and armatus are alleles. For example, when a female guppy carrying the coccineus-vitelinus pattern (linked to the X chromosome) is mated to a male carrying both the CoVi and Ma pattern, the expected CoVi and non-CoVi females plus CoVi-Ma and Ma-Ma were obtained. However, an unexpected male Ar-CoVi was also obtained, unexpected because armatus was nowhere in the cross.

SEX REVERSAL: There is evidence for a dual sex-determining mechanism in guppies which, in brief may be summarized as follows:

1. Female and male sex-determining genes are probably distributed over many autosomes being concentrated, however, in the sex chromosomes.
2. These superior sex genes in the sex chromosomes may upon rare occasion be overridden by those in the autosomes.

Thus, one may have XX male guppies and XY female ones. In other words, their genetic sex is opposite to their real sex. For example, when a male XX guppy carrying the Y1 pattern (a bright yellow caudal fin) on both chromosomes was mated with a normal XX female, the progeny were (as to be expected) all female. They all, however, carried the Y1 pattern through out after masculinization.

Such situations represent a precarious genetic balance, however, and the genetic pressure is such as to restore the normal state of affairs. The mechanism of a cross between two sex-reversed guppies is illustrated as follows. Colorless Ma female x non-Ma male = F₂ = colorless females + Ma males. There is, therefore, a canceling out of the influencing autosomal sex genes in both sexes and the sex-determining mechanism is restored once again to the sex chromosomes.

CONCLUSION: Without a doubt, the fact that a large number of polymorphic color patterns normally behave genetically as though linked to the Y chromosome, is an unusual situation among vertebrates. One experiment involving 44 wild males and subsequent analysis of 1,286 of their progeny, indicated that linkage tends to predominate in the Y chromosome.

TABLE 1 Linkage of Patterns Observed in Wild Males

Exclusively Y-linked	233
Exclusively X-linked	29
In both X and Y	20
Autosomally-linked	30

Note: The majority of autosomally-linked patterns were simple spots or stripes involving only melanin.

Under normal circumstances, therefore, there may be good reason to concentrate on the males rather than on the females during a breeding program. To a considerable extent, perhaps, the importance of the female in linebreeding programs (genetically speaking) may have been overemphasized. This is not to suggest, however, that the female be ignored, ent rely. As has been pointed out certain colors and patterns are either autosomally (e.g., golden, albino, etc.), X-linked (coccineus-vitelinus) or both X and Y linked (e.g., Sh. a blue saddle-like patch near the dorsal fin.) Furthermore, it has also been demonstrated that the inheritance of spine deformities is simple Mendelian in nature. The serious guppy specialist cannot afford to disregard those aspects of guppy genetics which are unusual, because it is precisely the unusual that he forever seeks.

"Genetics of the Guppy" by A.J. Klee, THE AQUARIUM, Apr. 1964 pps26-31

GROWTH PATTERN IN GUPPIES

By Henry Kaufman

Male guppies grow in three distinct stages and the whole process takes place in approximately nine months. In the first stage the major growth is in the BODY. In the second stage, the major growth is in the TAIL, and in the last stage the growth is in the DORSAL. From the time the fry are born and they are nine months old the body is continually growing. However, the most rapid growth is during the first three to four months. At the four-month level, the male's body growth will be about 70% completed. At this time the body rate of growth slows down and during the next four months, he should grow the additional thirty percent of this eventual size. At about the time the body growth rate begins to decline, the tail really starts to expand. Up to this point the tail should be about one-third size. The greatest rate of tail growth will be from the time the fish is four months old until he is six to seven months old. At this point, the growth should be about ninety percent complete. When the fish is six to seven months old, the body size should be there, and then the dorsal should spread. Up to this age the dorsal will be about sixty percent grown and the balance will grow during the next three months. For show purposes, this is the prime age of a fish. If at this age the fish does not have all three stages fully developed he will not be worth breeding.

From this analysis of the growth pattern of the male guppy, we can now point out certain facts which will aid us in selecting as well as rejecting certain fish. If the fish we are examining has a large dorsal, and minor body, we can assume that its growth is nearly complete and we can expect very little in the way of future body growth. If he has a small size tail and a large dorsal, we can discard him on the grounds that his tail will not be what we really are looking for. If, on the other hand, we find a few with extra large sized bodies, with very little size in the tail or dorsal, and they are at the three or four month stage we should watch these fish with great interest. Here is where you will find your future champion. At the early age, forget color, tail size and dorsal size. These will develop later on in the growth pattern. Concentrate on the ones with large bodies. Remember too that in order to be able to properly carry and swim with a large size tail and dorsal, the fish must have the right body size to support the added weight. Too many times we see fancy guppies who have large tails and dorsals struggling to swim in an upright position because they do not have the body size necessary to go with the tail and dorsal.

You will note that up to now we have mainly concerned ourselves with the growth pattern of the male. Now we take up the growth pattern of the female where we look for different indicators from those we watched for in the males. In the female, as in the male, the growth pattern will be about the same time, eight to nine months with the most rapid rate of growth occurring during the first three months. By the time the female reaches this age, we should concentrate on the largest sizes of the lot. These will have a chunky or hefty look to the eye, a comparison to the sisters of the same age. While the tail formation will not be large, it should not be rounded but should show a wide "V" spread such as you look for in the male. Try also to look for the females which have a hefty look in the dorsal. All these features will generally be found in the largest females of the brood.

One other vital factor that virtually controls the ultimate size of the female, can also be controlled at the early stage level. To a certain extent, the female will grow in direct relation to her food and environment. But more important is the fact that a female will grow in direct relation to the time at which she becomes pregnant for the first time. If you let her become pregnant at the age of one or two months, she will eventually grow to be two to three times the size she was at one or two months of age.

On the other hand, if you keep her barren until she is three or four months old, she will grow to be two to three times the size she was at the three to four month period. Keeping the female virgin longer than four months is not advisable since in most cases they lose or impair their ability to reproduce. This growth pattern in females is probably due to the fact that when a very young guppy becomes pregnant, half of the food she eats goes into building the babies and half into building her own body. If babies are not present, all the food she eats goes into building up her own body.

by H. Kaufman, THE AQUARIUM Feb. 1965

HYBRID VIM AND VIGOR

OPINION NUMBER ONE

by William L. Brown

George Shull's experiments with inbreeding and crossbreeding corn made it possible to feed the world.

For thousands of years Indians of the Western Hemisphere grew corn, varieties pollinated by the wind and bred largely by chance. Despite their lack of scientific insight they transformed a wild grass from Mexico into one of the world's most productive plants. Sixteenth and 17th century farmers continued the practice of corn improvement. Distinct varieties were developed by selecting the best ears at the time of harvest and using seed from those ears to produce the next year's crop. This kind of selection continued until about 1900 and resulted in scores of high-yielding, randomly pollinated varieties. Then, in the course of just a few years, student in applied genetics to corn breeding and brought about a transformation of agriculture in this century.

The development of hybrid corn resulted from the exploitation of a phenomenon known as HETEROZIS or HYBRID VIGOR. This increased yield, vigor, and rate of growth of plants comes from the mating of unrelated parents. Many early botanists and horticulturists, including Charles Darwin, had previously observed this phenomenon. But it was geneticist George Harrison Shull who developed the heterosis concept as it is applied today. He and E.M. East, a contemporary whose experiments at the Connecticut Agricultural Experiment Station in New Haven closely paralleled Shull's, were the first to isolate pure strains of corn. These were then crossed to produce the reliable vigor of hybrid corn.

Shull had the advantage of a number of discoveries relating to heredity that preceded him. Foremost was the recent rediscovery of Mendel's laws, which were not known to Darwin. There were also Darwin's classical greenhouse studies on the effects of self-fertilization, or inbreeding, and crossbreeding on corn plants. He observed that the progeny resulting from the mating of related strains did not exhibit the vigor of hybrids from matings of unrelated strains. In this way, he established that the mere act of crossing was not responsible for increased vigor in the progeny. Then in 1879 William James Beal, a follower of Darwin, made the first controlled crosses of varieties of corn in order to increase yields.

Beal did no inbreeding of corn and made no attempt to purify strains or to investigate their genetic basis. And so the stage was set for Shull to apply his knowledge of Mendelian laws of inheritance to hybrid corn.

Shull began his experiments to test the effects of cross and self-fertilization on the number of rows of kernels on ears of corn. During several years of work he developed a number of inbred strains by repeated self-fertilization, year after year, of the progeny from a single ear of white corn.

He observed that the progeny from these self-fertilized plants became smaller and weaker with each generation, though quite uniform. Shull also observed that the several inbred lines derived from a single open-pollinated, or randomly pollinated variety, differed markedly from each other in a number of physical characteristics, including the number of rows of kernels. Shull concluded that inbreeding or self-fertilization resulted in the isolation of pure, genetically uniform strains that could be used as parents to produce hybrids having specific desirable characteristics.

Shull next step was to cross two pure lines, each of which had different numbers of rows of kernels. The results led him to see the implication of his studies on corn breeding and corn improvement. He noted, for example, that the vigor lost as a result of self-fertilization was restored in the progeny when two unrelated pure lines were crossed. The plants of this first-generation hybrid were highly uniform in characteristics and higher yielding than either of the original open-pollinated varieties from which the pure lines had been developed.

These results were reported in two publications in 1908 and 1909. In a brief span of five years Shull established a sound biological basis for hybrid corn, completely changing the course of corn breeding and establishing a model for the improvement of many crops.

Donald F. Jones realized that the progeny of two pure, inbred strains called a **single cross** might be bred with another single cross. The result, he thought, of mating two single crosses would combine the outstanding characteristics of four inbreds rather than two, and would take advantage of the high yield of the single-cross seed parent, taking the best inbred strains he had, two parents from one variety and two parents from another. At harvest time he got a 20 percent better yield than the best of the varieties farmers were then using.

Although Jones' **double-cross method** was an essential step in the development of hybrid corn, few double-cross hybrids are now used. The development of more vigorous, higher yielding, inbred lines has made possible the commercial use of single crosses better than the best double crosses.

OPINION NUMBER TWO

by Ray D. Owen

HYBRIDIZATION OF INBRED LINES Hybrid Vigor in Corn you will recall after inbreeding over a period of generations leads to successive reductions in vigor. Sometimes, inbred lines die out entirely. Where they do not, a time comes when continued self-fertilization is accompanied by no increase in deleterious effects. Presumably this stabilization occurs when homozygosity is reached. You will not suppose, of course, that such a characteristic as yield will ever be entirely constant, even in a homozygous line. Yield, like most quantitative characters, is sensitive to fluctuations of environment and planting seasons differ sufficiently from one year to the next, to provide a basis for appreciable variation in phenotypic expression.

If two different inbred lines of corn are crossed, the hybrid progeny display heterosis. They are almost always strikingly more vigorous than their parents. Usually such hybrids are vigorous by any standards. But to clear up fairly common misconception, it should be said that hybrid corn plants are not unique in vigor or even markedly superior to the best plants of open-pollinated origin. In fact, certain open-pollinated plants are superior to many hybrids. The basic reason for the success of hybrid corn in our agricultural economy is that members of the F-1 hybrid group show a uniformity of high-level performance not found in open-pollinated varieties. After the F-1 generation, however, characters like height and yield are

not maintained at so high and uniform a level in a study the yield of ten different corn hybrids was compared in the F-1 and F-2 generations. The first generation hybrids gave an average yield in bushels per acre of 62.8; the average yield for the same hybrids in F-2 was 44.2. These results are typical. They should remind you of facts that emerged in the discussion of quantitative inheritance uncomplicated by heterosis (page 157). You will remember that for quantitative characters in general, the F-2 is much more variable than the F-1, and encompasses a whole spectrum of variation. Increased variability after the F-1 results from genetic segregation and recombination.

EXPLANATIONS OF HYBRID VIGOR: Heterosis is a phenomenon that is at once intriguing and practically important. It is manifested in different groups of organisms, being by no means confined to corn, or even to plants. No doubt what is called hybrid vigor in various groups of organisms is not everywhere the same phenomenon. But these various manifestations doubtless have much in common, and a satisfactory explanation of one will aid considerably in understanding other.

All attempts to explain hybrid vigor stem from one basic fact. This is, that the vigor is found associated with the heterozygous state. A synonym for hybrid vigor, already utilized, serves to emphasize this point. One of the pioneers of hybrid vigor in corn, proposed the term heterosis, a kind of contraction of heterozygosis, as a word likely to be useful in connoting the increase of size and vigor following cross. We will use heterosis and hybrid vigor interchangeably, as a common practice in the literature of genetics.

Most genetical theories designed to explain heterosis fall into one of two categories:

EXPLANATIONS BASED ON INTERACTION OF ALLELES. A number of geneticists have proposed, in one way or another, that heterozygosity per se is essential for heterosis. Reduced to simple terms, theories of this kind say that if there are the alleles a_1 and a_2 for a single locus, the heterozygous combination a_1a_2 is superior to either of the possible homozygotes, a_1a_1 or a_2a_2 . Obviously this is a kind of dominance interaction new to us. To express it, the term overdominance has been suggested. The implication is usually the alleles a_1 and a_2 , do separate things, and the sum of their different products or some reaction product between them, is superior for vigor to the single product produced by either allele in the homozygous state.

There is considerable evidence that different alleles at a single locus are indeed able to do different things. For example, in several organisms members of multiple allelic series have been found to produce different blood antigens. In heterozygous combination, each different allele can be shown to give rise to its own peculiar product. Also pertinent to the general argument is the fact that a number of instances have been described where a heterozygote gives more extreme phenotypic effects than either homozygote. Experiments give clear examples where heterozygosity per se results in a deviation more extreme than is produced by either homozygote.

Results bearing directly on the relationship of heterozygosity to vigor have come from the work of Ake Gustafsson, Sweden. He has utilized spontaneous mutations within pure lines; these permit the comparison of homozygotes and heterozygotes under conditions where the entire residual genotype is closely controlled. In the pure line variety of barley called Golden, he reported that heterozygotes for the chlorophyll mutants albino 7 and xantha 3 show consistent advantages over the homozygous normals in spike and kernel number and in kernel weight. The homozygous mutant types are lethal

similar to Gustafsson's have been described, but it is not yet known whether they are exceptional or whether they represent a situation of wide occurrence.

EXPLANATIONS BASED ON THE INTERACTION OF DIFFERENT DOMINANT GENES.

Many geneticists have felt that heterosis does not require overdominance, but that it can be rather simply be explained in terms of ordinary dominance of genes relatively favorable for vigor and the corresponding recessiveness of genes unfavorable for vigor. The reasoning behind this second kind of explanation can be most readily seen if we return to the effects of inbreeding.

We have already discussed how, in groups of organisms that are normally not inbred, deleterious recessive mutant genes may accumulate because they are masked by dominant normal alleles. Deleterious dominant mutations tend to be eliminated from populations rather rapidly because they are immediately and continually subjected to adverse natural selection. Among normally inbred groups, even deleterious recessives do not accumulate to any great degree. Inbreeding leads to homozygosity, and thus in these groups unfavorable recessives are subject to much the same sort of pruning through natural selection as occurs for deleterious dominants everywhere. This continual process of pruning away undesirable recessive genes in naturally self-fertilized organisms accounts for the fact that such plants as oats can maintain a level of vigor apparently as high as is found among naturally cross-fertilized plants.

If one makes a cross between unrelated inbred lines of corn, it is likely, indeed almost inevitable, that at particular loci the parent lines will differ depending on whether dominant or recessive alleles have become homozygous through the inbreeding process. Thus, if we were to designate five loci in a hypothetical cross between inbred, a representative situation might be as follows:

INBRED I (aaBBCCddEE) X INBRED II (AAbbCCdd ee)

F1 = (AaBbCCDdEe)

If the different recessive alleles are even mildly unfavorable to vigor, the hybrid having the relatively favorable dominant alleles at more different loci that is true for either inbred, should be more vigorous than either parental line. A look at the hypothetical cross will also help to make it clear how it is that uniformity is a characteristic of hybrid corn. Since the parental inbred lines typically are homozygous, their progeny must be genetically uniform. You realize of course, that this is not the same as saying the progeny are homozygous.

The above general explanation of heterosis is different in a fundamental way from the first kind of theory we discussed. Since in the second case it is assumed that heterozygosity is largely incidental to the phenomenon of hybrid vigor, it should be possible to obtain lines of corn that breed true for the vigor found in particular hybrids. For instance, the hypothetical F1 individuals AaBbCCDdEe, if intercrossed or self-fertilized, should give some progeny of the genotype AABBCCDDEE. Continued failure in actual experiments, to find true-breeding lines as vigorous as F1 hybrids might be taken as evidence in favor of theories based on allelic interaction. For if the heterozygous condition as such accounts for hybrid vigor, then this kind of vigor could not be expected to be stabilized in homozygous lines.

In corn, fixing the vigor of F1 hybrids into true breeding lines has not so far been possible. It has been pointed out, however, that the recovery of lines homozygous for all the favorable alleles for a multiple gene character may pose a herculean task for the plant breeder. If expression of vigor is influenced by genes at, say, thirty different loci in a hybrid, the probability of recovering one particular homozygous combination among the progeny $\frac{1}{2^{30}}$

